

REVISION OF SOUTH AMERICAN TITANOSAURID DINOSAURS: PALAEOBIOLOGICAL, PALAEOBIOGEOGRAPHICAL AND PHYLOGENETIC ASPECTS

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ABSTRACT

The titanosaurid dinosaurs (Saurischia-Sauropoda) are well represented in South America, playing an important role in the Late Cretaceous ecosystem as gigantic herbivores, an adaptive zone which evidently they alone occupied for the greater part of the period. Specimens assignable to this family have been found at 50 South American localities, 28 from Argentina, 7 from Brazil, 12 from Uruguay, 2 from Chile and 1 from Peru. For each of these localities the geographic location, lithology, associated fauna, and occasionally the associated flora is given.

In the systematic section, the family Titanosauridae is redefined. The principal diagnostic characters being the possession of markedly convex posterior articulation on the centra of the caudal vertebrae, and the cervical, dorsal and occasionally caudal vertebrae having well developed cancellous tissue and extremely thin sheets of compacta. Skull with large and recurved paroccipital process and short basiptyergoid process. The following taxa are briefly described: *Titanosaurus araukanicus* (Huene 1929a), *Aeolosaurus rionegrius* Powell 1987b, *Saltausaurus loricatus* Bonaparte and Powell 1980, *Neuquensaurus australis* (Lydekker, 1893), *Argyrosaurus superbus* Lydekker 1893, *Epachiosaurus sciutoi* Powell 1990 and *Pellegrinisaurus powelli* Salgado 1996.

Titanosaurus nanus Lydekker 1893, *Microcoelus patagonicus* Lydekker 1893, *Neuquensaurus robustus* (Huene 1929a), *Antarctosaurus brasiliensis* Arid and Vizotto 1971 and *Clasmodosaurus spatula* Ameghino 1898 are considered as *nomina dubia*.

Biomechanical aspects of the skeleton of the titanosaurids are analyzed, in particular the gigantic size and the adaptations for offsetting and reducing weight. In the general manner of graviportal animals, they have vertical, columnar limbs in which the humerus and femur are longer than the ulna-radius and the tibia-fibula.

Briefly, the different parts of the skeleton are examined. The axial skeleton decreases its weight by evolving the spongiosa in large cavities in the place of the large pleurocoels of other sauropods in the centra of the vertebrae and the dorsal splitting (dorsally split neurapophysis) of the neural arch of the cervical, dorsal and anterior caudal vertebrae. Dorsal vertebrae show the greatest development of bony laminae between the dorsal split of the neural arch which reduces to a minimum the weight of the bone, while maintaining the structural strength necessary for mechanical efficiency.

The sacrum and ilium form a strongly co-ossified structure. The sacral ribs have an 'I'-shaped profile. The ilium is markedly expanded towards the anterior and outside. The morphology of the acetabulum suggests that the sacrum is inclined enough towards the posterior to allow the possibility that these animals occasionally adopted a bipedal posture, the anterolateral expansion of the lamina of the ilium served as a large lever arm to control movement in the sagittal plane.

The titanosaurids are recorded at diverse localities in South America, North America, Europe, Africa, Madagascar and India. This is evidence for geographic links in the late Cretaceous between South America, India and Africa-Madagascar and possibly with Europe (via Africa) and North America.

The diet of the titanosaurids was undoubtedly herbivorous. The teeth are generally cylindrical (except *Malawisaurus* Jacobs et al. 1993 and *Ampelosaurus atacis* Le Loeuff 1995) with well developed apical wear facets, oblique to tooth axis. These facets were the result of tooth to tooth contact while feeding.

A phylogenetic analysis of titanosaurid dinosaurs is included as an appendix. According to this analysis, *Opisthocoeleicaudia* is the closest sister group of Titanosauria (*Epacluhosaurus* (*Alamosaurus* + *Lirainosaurus* + *Peirópolis* titanosaur (*Aeolosaurus* (*Saltasaurus* (*Argyrosaurus* (*Titanosaurus colbertii* + *Ampelosaurus*)))))). This clade is mainly characterised by the presence of a flat horizontal surface at the end of diapophysis on posterior dorsal vertebrae (paralleled in *Haplocauhosaurus*), the presences of developed posterior condyles in the centra of anterior caudal vertebrae, and an anteroventral ridge in the sternal plate. Another clade includes all the derived forms, traditionally considered as titanosaurids (Eutitanosauria): (*Alamosaurus* + *Lirainosaurus* + *Peirópolis* titanosaur (*Aeolosaurus* (*Saltasaurus* (*Argyrosaurus* (*Titanosaurus colbertii* + *Ampelosaurus*)))))). This taxon is diagnosed by the absence of a hyposphene-hypantrum articulation in posterior dorsal vertebrae, a reduced fourth trochanter in the femur and presence of osteoderms documented in Argentina, Brazil, Spain, France and Madagascar.

I. INTRODUCTION

Although Upper Cretaceous dinosaurs, and sauropods in particular, are among the first fossil tetrapods to be found in South America, around a century ago, they are yet an insufficiently known group.

Titanosaurids are basically quadrupedal, herbivorous dinosaurs. This group survived up to the Late Cretaceous of South America and other areas of the world. Although titanosaurids have been recorded from North America, Europe, Africa, Madagascar and India, they are poorly known the world over. South America is the continent from which the fossil record is more abundant and complete.

Studies by Lydekker (1893) and Huene (1929a) based their observations on collections mostly from Patagonia. Their work was in many cases difficult owing to the fact that specimens were fragmentary and poorly preserved, many collected by geologists and curious travellers, who collected specimens disturbed by erosion. Others, came from fossil-rich deposits, such as Cinco Saltos (Huene 1929a) and General Roca (Wichmann 1916) in Río Negro Province, consisting of important bone accumulations from disarticulated skeletons. In both cases, numerous complete parts belonging to several individuals of two or three different genera, were scattered about the area. This forced the investigators to use arbitrary criteria in grouping the elements which might have belonged to any taxon known to be present (Huene 1929a).

The basis established by Huene (1929a) and Lydekker (1893) through their valuable work, still holds with modifications of some of the nomenclature. Some reconsiderations concerning the validity of some taxa and interpretations on the anatomy and palaeobiogeographic implications have been made.

The rich titanosaurid record in South America, and in particular the new material discovered because of the reactivation of palaeontological exploration in various parts of South America (mainly Patagonia, north-western Argentina, and Brazil), have fostered the present work in which a revision of the Titanosaurid family is given. It is based on already described as well as unpublished material, reinterpreting aspects related to taxonomy, anatomy, palaeoecology and palaeobiogeography.

The present revision demonstrates the breadth of diversity of the group in South America, and evaluates the taxonomic assignments made on previously studied specimens. Nonetheless, the fragmentary nature of the available evidence makes this preliminary study subject to modification through the discovery of more complete material.

Descriptions have been emphasised owing to the abundance of the available material. In the case of some forms, there are brief observations highlighting some characters considered of interest by the author.

Supplementing the descriptions are a set of illustrations consisting of drawings and photographs of part of the material discussed.

The excellent material of Minas Gerais (Brazil) has been studied in a preliminary manner but needs further investigation. Here this material has been identified at the generic level in most cases. It has also been employed to illustrate aspects of vertebral morphology, e.g. number and variation throughout the axial skeleton.

This is documented for the first time in this group on the basis of well preserved articulated material.

In Chapter 8 some biomechanical aspects stemming from the observation of certain anatomical peculiarities of sauropods (particularly of titanosaurids) are analysed. Because of their great weight, these animals have evolved peculiar structures. Available bibliographic data concerning dinosaur biology, based on observations carried out on materials assigned to titanosaurids, was the means of producing a preliminary and partial account of their paleobiology.

Chapter 10 is a brief review of the extra South American sites, which have yielded titanosaurid remains, together with an analysis of the palaeogeographic and palaeobiogeographic implications of their distribution.

When the core of this work for a PhD dissertation (Powell 1986) was concluded, there were few well represented available taxa. New important findings and studies have provided additional data about the morphological features of the group. Based on this new

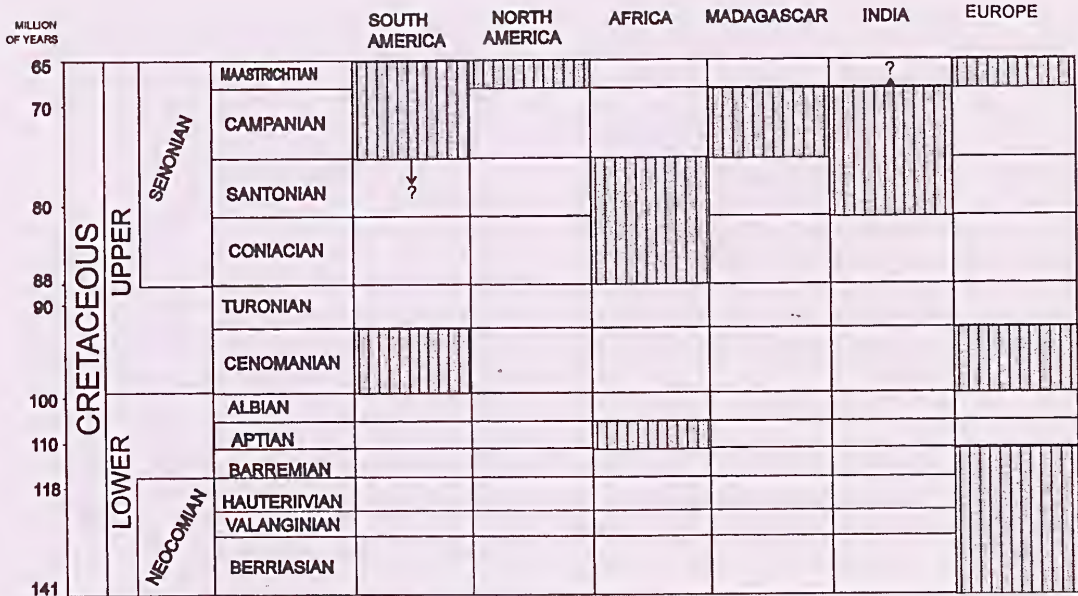


Table 1. Chronological ranges of the Titanosauridae on various land masses depicted by stippled rectangles with closely spaced vertical lines.

evidence, a phylogenetic appendix is included. This analysis is largely based on Sanz et al. (1999). Some characters included in the matrix have been changed and several genera not considered in the previous work have been added.

In many cases, there are problems impossible to resolve at present, which might be solved with new discoveries of articulated specimens or at least associated ones.

Several areas are pointed out in which doubts can be resolved through future study. To avoid going beyond the bounds of the available geographic and stratigraphic evidence, a limit must be placed on the original claims of this work.

II. HISTORY OF RESEARCH ON THE TITANOSAURIDAE

The oldest descriptions of specimens belonging to the family Titanosauridae were based on the discovery of bones in peninsular India. The first references date back to 1862 when Hugh Falconer described two caudal vertebrae in which he recognised reptilian affinities.

Hislop (1864) makes reference to a discovery at the Pisdura site, central India, among which were vertebrae and a femur that certainly belonged to titanosaurids. Although these specimens seem to be missing (Pascoe 1963), more material continued to be found. Falconer's specimens were re-studied by Lydekker (1877) who immediately deduced from comparisons that the vertebrae were from the caudal region of a dinosaur. On this basis he founded a new genus and species: *Titanosaurus indicus*. Lydekker (1879) re-described

Titanosaurus indicus, reproducing the illustrations of Falconer (1868), and described another species: *Titanosaurus blandfordi* coming from the Lameta Group in Pisdura. He also discussed the caudal vertebrae. The first reference concerning large dinosaurs in South America goes back to 1883, when Florentino Ameghino published an article about the discovery of these large reptiles in the daily 'La Nación' on the 23rd of March of the same year. Two years later, Ameghino (1885) inferred an Upper Cretaceous age for these dinosaur-bearing strata.

The first specific study of them based on Argentinian and South American material was made by Lydekker (1893), who described specimens from the Neuquén Group and the Chubut Group, collected by Santiago Roth, Carlos Ameghino and others. He named various genera and species: *Titanosaurus australis*, *?Titanosaurus nanus*, *Microcoelus patagonicus* and *Argyrosaurus superbus*. Lydekker (1893) pointed out the affinities of these with the previously described forms from the Cretaceous of India and proposed the erection of the family Titanosauridae for this group of dinosaurs with their peculiar characteristics.

Huene (1927) published a succinct revision of the sauropods including a diagnosis of the family Titanosauridae and a list of the recognised genera pertaining to the same. Later, Huene (1929a) published an extensive and valuable monograph about the dinosaurs of the Late Cretaceous of Argentina. This is considered the basic work concerning the subject in South America. It is devoted mainly to the family Titanosauridae. It includes detailed descriptions and a revision of the specimens

available at that time at the Museo de La Plata and the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' of Buenos Aires.

The research on the Late Cretaceous sauropods of Argentina ceased for several decades. Active investigation resumed when Bonaparte and Bossi (1967) made known for the first time the presence of titanosaurs in the Salta Group in north-western Argentina. Bonaparte et al. (1977) discussed for the first time the discovery of armoured Titanosauridae coming from that region, associated with the remains of carnosaurs, coelurosaurids, and birds. Preliminary descriptions of dinosaurs were made by Bonaparte and Powell (1980).

Among the authors who discussed general aspects of the family Titanosauridae in South America, mention must be made of Bonaparte (1978), who synthesised the information concerning fossiliferous areas of the Late Cretaceous that have yielded titanosaurs in South America.

Bonaparte and Gasparini (1979) presented an update of the Late Cretaceous sauropods of Argentina. They indicated the stratigraphic provenance of some of the old discoveries and proposed lectotypes for some taxa that lacked formally designated types. In addition, these authors discussed the validity of the considered taxa, and proposed the correlation of the units of the Chubut Group and the Neuquén Group, based on the presence of similar titanosaurs found in both basins.

Recent findings and valuable studies of Cretaceous sauropods (including titanosaurs) of Argentina and other non-South American localities have contributed to the improvement of the knowledge of the group. These contributions include new approaches to sauropod phylogeny focused mainly on the titanosaurs (Calvo & Bonaparte 1991; Bonaparte & Coria 1993; Salgado & Bonaparte 1991; Calvo & Salgado 1995). Some authors studied some aspects of the palaeobiology of titanosaurs and other sauropods, e.g. jaw mechanics by Calvo (1994a, b).

Besides the studies on Argentinian titanosaurs, other researchers worked on material found in other South American countries. Price (1951, 1955), Mezzalana (1959, 1974) and Arid and Vizotto (1971) studied material from Brazil; titanosaurid remains from Chile were considered by Casamiquela et al. (1969) and Chong Díaz (1985) while those of Uruguay were studied by Huene (1929a). Additional references related to the history of discovery and titanosaurid studies are included below. McIntosh (1990) reviewed the Sauropoda of the world including the titanosaurs. Upchurch (1994, 1995) studied the Sauropoda using a cladistic approach, including a synthesis of the phylogenetic hypotheses previously considered.

Knowledge of European titanosaurs recently greatly improved owing to new findings in Northern Spain

(Casanovas-Cladellas et al. 1995; Sanz et al. 1999) and southern France (Le Loeuff 1993 1995). New discoveries from Africa (Jacobs et al. 1993) and India (Jain & Bandyopadhyay 1997) provided extremely valuable information concerning titanosaurs.

III. MATERIALS AND METHODS

A. Materials

This revision is based on the study of material of the collections housed in museums of Argentina (Fundación Miguel Lillo (Tucumán), Museo de La Plata, Museo Argentino de Ciencias Naturales 'B Rivadavia' Buenos Aires, Museo Provincial 'Carlos Ameghino' (Cipolletti, Río Negro), Museo 'Professor Oscar Olsacher', Museo de Ciencias Naturales de la Universidad Nacional del Comahue, (Neuquén), Brazil (Museo de la Divisão de Geologia y Mineralogia of Rio de Janeiro), Uruguay (Museo Nacional de Historia Natural of Montevideo, Museo Municipal 'A. Berro', Mercedes), the United States (Field Museum of Natural History, Chicago), and England (Natural History Museum, London).

Collections of non-South American titanosaurs and other related sauropods of North America, Europe, Africa and Asia were consulted in the following institutions: National Museum of Natural History, Washington, DC, United States; Natural History Museum, London; Muséum National d'Histoire Naturelle, Paris; Musée des Dinosauriens, Espéraza, France; Facultad de Ciencias de Universidad Autónoma de Madrid and Museo de Ciencias Naturales de Alava, Spain.

In these institutions I have made observations, achieving a clear understanding of the variety of forms that integrate the family in South America and the rest of the world, resolving some important nomenclatural problems and considering general morphological aspects about titanosaurs.

The following abbreviations are used to indicate the repositories of materials figured in the text and correspond to the following institutions:

BMNH	Natural History Museum, London.
CNS-V	Colección de Paleontología de Vertebrados de la Facultad de Ciencias Naturales de la Universidad Nacional de Salta.
DGM	Museo de la Divisão Geologia y Mineralogia de Dir. Nac. Prod. Mineral, Rio de Janeiro, Brazil.
FFCL	Faculdade de Filosofia, Ciências e Letras de São do Rio Preto.
FMNH	Field Museum of Natural History, Chicago.
MACN	Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'.
MCT	Earth Sciences Museum of National Department of Mineral Production, Rio de Janeiro.
MJG	Museo Jorge Gerold, Ingeniero Jacobacci, Río Negro.
MLP	Museo de La Plata, La Plata.

MMAB	Museo Municipal 'Alejandro Berro', Mercedes, Uruguay.
MNHM	Museo Nacional de Historia Natural de Montevideo
MPCA	Museo Provincial 'Carlos Ameghino', Cipolletti, Río Negro.
PVL	Colección de Paleontología de Vertebrados de la Fundación Instituto Miguel Lillo, Tucumán

B. Methods

Traditional methodology for palaeontological investigations in descriptive, comparative and interpretive aspects was used. With respect to the considerations of phylogenetic interpretations I have utilised some principles of the cladistic method for analysis in reference to the polarization of characters, with comparison to outside groups

Descriptions

For the descriptive work the skeleton of the titanosaurids is considered in natural position, this is with the limbs more or less vertical, placing the bones anterior, posterior, dorsal or superior, and ventral or inferior in this scheme, which corresponds in general to the reconstruction of the skeleton of *Saltasaurus loricatus* shown on plate 1.

Measurements

The measurements which are given in Tables 2–31 were taken according to the scheme in Plates 2–4, whose abbreviations are explained in the picture captions.

There are cases where measurements are impossible, owing to problems of preservation or feasibility of measurement which are explained in the corresponding tables.

An index of robustness (IR) in long bones has been determined in almost all cases, which is obtained by the following relation: $IR = P_{smn}/L$, where P_{smn} is the perimeter of the smallest section, for the reason that it is the measurement least affected by deformation (McIntosh, pers. comm.), and L is the length.

Taxonomic work

As far as the taxonomic work is concerned, the question mark is used to indicate a dubious assignment to a certain taxon. Komicker's (1979) proposal of putting a question mark immediately behind the taxonomic name which is in doubt, is followed.

For example:

Titanosaurus? australis Lydekker.

Species questionably assigned to the genus.

Titanosaurus australis? Lydekker.

Species dubious, generic assignment correct.

?*Titanosaurus australis* Lydekker.

Generic and specific assignment dubious.

Cladistic analysis

The phylogenetic analysis is presented as a Phylogenetic Appendix. This study is mainly based on a contribution by Sanz et al (1999). Most of the characters considered in

that paper were used here, but other South American, Indian and European taxa were added. The matrix of plate 86 has been processed using NoNa and Hennig 86 with exactly the same results. More details about the methods used are given in the Phylogenetic Appendix.

Illustrations and photographs

Some drawings, such as the cranial specimens of *Antarctosaurus wichmannianus* and *Saltasaurus loricatus* were made from photographs, which accounts for the differences in scale in the different planes of the drawing.

The rest of the illustrations have been drawn directly from original material, except when indicated in the respective captions.

The photographs have the scale indicated on the figures. They were made in traditional fashion in so far as possible, but experienced some anomalies owing to technical reasons (size of specimens, conditions of natural or artificial illumination, etc.).

IV. SOUTH AMERICAN FOSSILIFEROUS LOCALITIES WITH TITANOSAURIDS

Although titanosaurid dinosaurs are known from many parts of the world, South America is the place where the record is most abundant and varied. The fossiliferous localities with titanosaurids correspond to Late Cretaceous sedimentary basins mostly concentrated in the southern part of South America (Map 1). Following the nomenclature used by Malumíán et al. (1983), these areas of Late Cretaceous sedimentation are: the Neuquina, San Jorge, Austral, Subandina basins (Argentina), an area of Mesozoic deposition of limited thickness over the Macizo of Somón Curá, (Argentina), Guichón-Yerúa Basin (Argentina and Uruguay), Baurú Basin (Brazil), and Andina Basin (Chile). However the most abundant and diverse record is that of Argentina and Brazil.

The most northern localities are those of Minas Gerais, Brazil, situated at approximately 20° south. The most southern occurrence of titanosaurids is close to Lago Argentino situated at 50°30' in Santa Cruz Province (Argentina). The Campanian–Maastrichtian levels present in these Cretaceous basins are the richest in fossiliferous localities in South America (Table 1). However, several discoveries of sauropods in older sedimentary units below the Campanian–Maastrichtian formations in the Neuquina Basin provide important evidence for the evolution of the Cretaceous sauropods in South America (Calvo & Bonaparte 1991; Bonaparte & Coria 1993; Calvo & Salgado 1995; Bonaparte 1996)

A. ARGENTINA

1. The Subandina Basin

The Subandina Basin extends through the territories of Argentina, Bolivia and Perú. Its southern sector is in Jujuy, Salta, and Tucumán provinces, where there are three fossiliferous localities with titanosaurid dinosaurs.

All are situated close to the southern margins of the basin (in the southern region of Salta Province): Arroyo Morterito, El Brete and Arroyo Potrero del Nogalito.

a. Arroyo Morterito, El Ceibal, Province of Salta (Map 2).

History

Mr Fidel Leal, the owner of the Finca Potrero del Nogalito, recognised the first fragments of bones obtained at this site. Palaeontologists from the Fundación Miguel Lillo initiated excavations in 1966. In addition they carried out a second stage, ending in 1975, during which they obtained more titanosaurid remains, including a premaxilla.

Bonaparte and Bossi (1967) reported the discovery and the geology of the area. This was the first record of Cretaceous dinosaurs in north-western Argentina. Based on the titanosaurids, these authors correlated the deposits in which they occurred with those of the Upper Cretaceous of Patagonia.

Powell (1978, 1979) re-studied the geology and the material previously described as well as the additional specimens collected in 1975, reporting an association of both sauropod and theropod dinosaurs.

Geographic Location

This locality is situated at the foot of the Sierra de Candelaria or Castillejo, 10 km to the south-east of El Ceibal, Department Candelaria, Province of Salta. The site is located on the right side of the Arroyo Morterito, on the Potrero del Nogalito, a ranch belonging to the Leal family.

Stratigraphic Position

The fossiliferous level corresponds to the upper section of the Los Blanquitos Formation (Pirgua Subgroup, Salta Group), as was suggested by Reyes and Salfity (1973) and later by Powell (1979).

Age

Late Cretaceous, Late Senonian, and Campanian. Bonaparte and Bossi (1967) assigned to the Senonian the upper portion of the Pirgua Subgroup (Reyes & Salfity 1973) on the basis of dinosaurs at the Arroyo Morterito locality. Los Blanquitos Formation is referred to the Campanian, because of the Campanian age estimated from radiometric dates for the underlying Las Curtimbres Formation (Reyes & Salfity 1973, Valencia et al. 1976) and the ?Campanian–Early Maastrichtian age suggested for the overlying Lecho Formation and the Yacoraite Formation (Maastrichtian) at El Brete (in this chapter).

Lithology

Light greyish-red conglomeratic sandstones. The bones were found as an accumulation of disarticulated elements, strongly affected by extreme abrasion, which occurred before burial. The sedimentary sequence suggests a fluvial environment with anastomosing channels close to areas of deposition.

Faunal List of the Locality

Sauropoda

Titanosauridae

Titanosaurus? sp.

Titanosauridae indet.

Theropoda incertae sedis

Unquillosaurus ceibalensis Powell 1978.

b. El Brete, Salta Province (Map 3)

History

The area of El Brete was studied after the discovery of radioactive bones reported by Danieli et al. (1960). Poor preservation and incompleteness of the material prevent the recognition of the taxonomic group to which they pertained. In 1975 a team from the Fundación Miguel Lillo, directed by Dr JF Bonaparte, located an accumulation of bones in the Estancia 'El Brete', close to the Arroyo González. The site is close to the top of a small hill, near a limestone quarry. The work in the area was continued during several months of that year and the two years following, resulting in a large and exceptional collection of dinosaurs and birds. The discovery was published by Bonaparte et al. (1977), giving an outline of the geology of the area and a description of the sedimentary sequence. Later, Bonaparte and Powell (1980) described the titanosaurid *Saltasaurus loricatus* and the small theropod *Noasaurus leali*. They also mentioned the presence of carnosaur and avian remains.

Walker (1981) made a preliminary study of the bird specimens found in association with the titanosaurids; the outstanding combination of peculiar characters justified their inclusion in a distinct subclass: Enantiornithes. Chiappe (1993) studied more avian material from this locality and reported three genera of Enantiornithes.

Geographic Location

The site is 500 m to the east of a limestone quarry situated close to Arroyo González on the Estancia 'El Brete'. This establishment is located 11 km west of El Tala, upon National Route 9 in the Department of Candelaria, in southern Salta Province.

Stratigraphic Position

Lecho Formation, Balbuena Subgroup, Salta Group. The fossiliferous level lies 22 m above the base of this unit.

Age

Late Cretaceous, Senonian, ?Late Campanian – Early Maastrichtian. There is a close similarity between *Saltasaurus loricatus* and *Neuquensaurus australis*, from the Río Colorado Formation (Campanian) and the Allen Formation (Early Maastrichtian) in the Neuquina Basin. This fact, and the absence of closely related titanosaurids in the earlier formation, suggests a Campanian–Maastrichtian age for the Lecho Formation. This unit at El Brete lies on the Yacoraite Formation that is equivalent in Bolivia to the El Molino Formation that is partly Maastrichtian in age (De Muizon et al. 1983). The

Lecho Formation must be restricted to the Early Maastrichtian or, with less probability, the Late Campanian, having in all appearances the Campanian age of the Las Curtiembres Formation as determined on the basis of radiometric datings, (Reyes et al. 1973, Valencio et al. 1976) and the age suggested in this work for the Los Blanquitos Formation. This interpretation is consistent with the correlation of the Yacoraite Formation to the Allen and Jagüel Formations as suggested by Powell (1980). The deposition of those units is probably related to the same transgressive episode. The titanosaurid remains found at El Brete were used by Bonaparte et al. (1977) to infer the age of the Lecho Formation as Late Senonian or probably Maastrichtian.

Lithology

Light greenish-grey fine sandstones, characterised by a coarse irregular stratification. Some banks present irregular cross-bedded stratification and bioturbation. Bossi in Bonaparte et al. (1977) has interpreted this sequence as corresponding to a fluvio-lacustrine coastal plain with frequent shallow lakes.

Faunal List of the Locality

Sauropoda

Titanosauridae

Saltausaurus loricatus Bonaparte and Powell 1980

Theropoda

Noasauridae

Noasaurus leali Bonaparte and Powell 1980

Theropoda indet.

Aves

Enantiornithes

Enantiornis leali Walker 1981

Soroavisaurus australis Chiappe 1993

Yungavolucris brevipedalis Chiappe 1993

Lectavis bretincola Chiappe 1993

c. Arroyo Potrero del Nogalito El Ceibal, Salta Province (Map 2)

History

The first indication of vertebrate fossil remains was found in 1977 (Powell 1978). Isolated bones of various sizes were found at this site, ranging from small bird to sauropod bone fragments.

Geographic Location

This site is located 500 m to the north of the confluence of the Arroyo Potrero del Nogalito and the Arroyo El Churqui, close to the Sierra de Candelaria or Castillejo, about 10 km from the locality at El Ceibal, Department of Candelaria, Province of Salta. This place is situated on the eastern side of a small hill that separates those arroyos.

Stratigraphic Position

Upper levels of the Los Blanquitos Formation (Pirgua Subgroup, Salta Group). The fossiliferous level is located above that containing the fossils of the Arroyo Morterito,

and is found immediately beneath the coloured 'brick red' levels that characterise the top of the formation at this place.

Age

Late Cretaceous, Late Senonian, possibly Campanian.

Lithology

Light greenish-grey fluvial sandstones, with abundant remains of transported bones. A wide range of sizes of bones is preserved, from fragments of titanosaurid elements of around 60 cm to small avian or reptilian bone fragments 1 mm in size.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

Theropoda indet.

Aves indet.

2. The Guichón-Yerúa Basin

This area of Late Cretaceous deposition includes part of the 'Mesopotamia Argentina' and the western region of Uruguay. Titanosaurid remains were found in this basin both in Argentina and Uruguay.

a. Calera Barquín, Entre Ríos Province

History

The presence of dinosaur remains in Entre Ríos Province was mentioned by De Carlés (1912). He found an incomplete humerus of a titanosaurid on the banks of the Río Uruguay between Concordia and Colón. Huene (1929a) offered some additional data to the comments made by De Carlés and described the available material. According to Frenguelli (1939), later discoveries were made in the area but there are no references to the material or its final repository.

Geographic Location

The site is located near the town of Calera Barquín, above the right bank of the Río Uruguay, to the north of the Colón locality, Colón Department, Entre Ríos Province. The place is accessible when the water level is low (Huene 1929a).

Stratigraphic Position

Puerto Yerúa Formation (Alba & Serra 1959) in Gentilli and Rimoldi (1979).

Age

Late Cretaceous, Senonian (Frenguelli 1939).

Lithology

'Lenticular red clay' (Huene 1929a).

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

This specimen was doubtfully referred to *Argyrosaurus superbus* by Huene (1929a, p. 81, Pl. 37: 4). However, there are not sufficient diagnostic features to assign this element to any known Titanosaurid genus.

3. The Neuquén Basin

a. Neuquén, Neuquén Province.

History

Commander Buratovich made the earliest discoveries in 1882. According to Huene (1929a) this army officer gave the fossil material to President Julio A. Roca, who put it in the hands of Florentino Ameghino. This investigator recognised that it pertained to dinosaurs and published a notice in the newspaper 'La Nación' on 23 March 1883.

Other specimens obtained from this locality were sent in 1887 by Coronel Antonio Romero, Commander of Neuquén. Lydekker (1893) studied these specimens and additional material collected by Santiago Roth, and described the titanosaurs *Microcoelus patagonicus* and *Titanosaurus australis*.

The construction of the railroad line Ferrocarril del Sur in 1887, resulted in the discovery of a large femur in this area, assigned by Huene (1929a) to *Argyrosaurus* sp. 'Boca del Sapo' is the site mentioned by (Huene 1929a). The snake *Dinilisya patagonica*, Woodward (1901) and the crocodiles *Notosuchus terrestris* and *Cynodontosuchus rothi*, described by Woodward (1896) were found in this area (Pascual et al. 1978). In this work, 'Boca del Sapo' is included in the area named 'Neuquén'.

Geographic Location

This is an area with extensive outcrops situated above the right bank of the Río Neuquén shortly before its confluence with the Río Limay. This area, known long ago as 'Sierra Roca', was crossed by people going to the west of the Neuquén and Limay rivers.

The area is progressively covered by the expansion of the city of Neuquén to the north. Important remains of snakes, birds, and crocodiles were found in the outcrops close to the campus of the Universidad Nacional del Comahue.

Stratigraphic Position

Río Colorado Formation, Lower La Carpa Member? (Bonaparte & Gasparini 1979).

Age

Late Cretaceous, pre-Maastrichtian Senonian (Digregorio & Uliana 1980), Campanian? (Uliana & Dellapé 1981). The pre-Maastrichtian Senonian age was deduced from the stratigraphic relationship of the sediments of the Neuquén Group, situated above the Rayoso Group which is dated as Aptian-Albian (Musacchio & Palarmaczuc 1975; Volkheimer & Salas 1976) and are underneath the Allen and Jagüel Formations of Early Maastrichtian Age (Bertels 1969; Ballent 1980). Traditionally it has been proposed that the maximum age for the Neuquén Group

was Coniacian-Santonian but it is evident from the unconformity that it is Senonian (Cazau & Uliana 1973). A Campanian age is inferred because the Maastrichtian Allen and Jagüel Formations overlie it (Uliana & Dellapé 1981).

Characteristics of the Sediments

Red sandstones, with remains of dinosaurs and silicified wood (Roth, 1899).

Faunal List of the Locality

Sauropoda

Titanosauridae

Neuquensaurus australis (Lydekker)

Titanosaurus sp.

cf. *Argyrosaurus* Lydekker

Theropoda

?Ceratosauria

Velocisauridae

Velocisaurus unicus Bonaparte 1991

Alvarezsauria

Alvarezsauridae

Alvarezsaurus calvoi Bonaparte 1991

Carnosauria indet.

Crocodylia

Notosuchia

Notosuchus terrestris Smith Woodward
(Huene 1929a; Gasparini 1981)

Comahuesuchidae

Comahuesuchus brachybuccalis
Bonaparte 1991

Baurusuchidae

Cynodontosuchus rothi Smith
Woodward (Huene 1929a; Gasparini
1981)

Ophidia

Dinilysidae

Dinilysia patagonica Smith Woodward
(Huene, 1929a; Bonaparte 1991)

Aves

?Ornithurae

Patagopterygiformes

Patagopteryx deferrariissi Alvarenga
and Bonaparte (1992)

b. Aguada del Caño

History

This locality was worked by Roth and Schiller in 1921 and 1923, during expeditions conducted for the Museum de La Plata. The specimens collected from this site were studied by Huene (1929a).

Geographic Location

This site is located 15 km to the north of China Muerta, on the road approximately halfway between Senillosa and Plotier, Confluencia Department, Neuquén Province. This locality was incorrectly located by Pascual et al. (1978), when they placed it much further to the south.

Stratigraphic Position

Río Neuquén Formation, Plottier Member? (Pascual et al. 1978).

Lithology

Coarse sandstones of grey, brown and red colours (Huene 1929a).

Age

Late Cretaceous, Senonian and pre-Maastrichtian (Pascual et al. 1978; Digregorio & Uliana 1980).

Faunal List of the Locality

Sauropoda

Titanosauridae

'Antarctosaurus' giganteus Huene 1929a

Titanosaurus sp.

Carnosauria indet.

Chelonia indet.

c. Cinco Saltos, Río Negro Province (Map 4)

History

Systematic excavations in the Cincos Saltos area were carried out by expeditions of the Museo de La Plata, directed by Roth and Schiller, during 1921 and 1923. The abundance of material found in these deposits induced Dr LM Torres to invite Dr F von Huene to study these specimens, which resulted in the classic monograph published later by Huene (1929a). Other specimens were discovered during construction of a large irrigation canal situated close to the city of Cinco Saltos (Torres 1950 in Andreis et al. 1974). However, this fossil was found in the underlying unit (Río Colorado Formation).

Geographic Location

Various sites were discovered some distance from the left bank of the canal that passes to the west of the city of Cinco Saltos, General Roca Department, Río Negro Province. There are sandstone outcrops of the Allen Formation that are found in many shallow gorges. The site worked by the crew of the Museo de La Plata was probably near to the present location of the industrial establishments INDUPA and BONANZA.

Stratigraphic Position

Lower member of the Allen Formation (Andreis et al. 1974). Other specimens were found in the Anacleto Member of the Río Colorado Formation, (Torres 1950 in Andreis et al. 1974).

Age

Late Cretaceous, Early Maastrichtian (Ballent 1980). Uliana and Dellapé (1981) have estimated for this formation a Campanian–Maastrichtian age. The formations in this basin have the Jagüel Formation lying above them, which contains Middle Maastrichtian foraminifers. The association of foraminifera coming from the upper levels of the Allen Formation in the Lago Pellegrini area, is comparable to what is known of the

upper member of the Huitrainco Formation with an Early Maastrichtian age. A similar age is inferred for the Allen Formation (Ballent 1980).

Lithology

Fluvial medium to coarse yellow sandstones.

Fauna listed from the Locality

Sauropoda

Titanosauridae

Neuquensaurus australis (Lydekker 1893)

Titanosaurus araukanicus (Huene 1929a)

Coelurosauria indet.

d. Aguada de Menéndez, Neuquén Province

History

The only available remains from this locality consist of a group of incomplete pieces of a juvenile titanosaurid. These include four caudal vertebrae, a fragment of an ilium or ischium, two femora, the distal two-thirds of a fibula and various metatarsals. Also found are very fragmentary material of a small theropod, probably a coelurosaurid and plates of a crocodile. These specimens are deposited in the collections of the Paleontología Vertebrados Lillo. Those were discovered in 1976 in the course of a campaign of exploration directed by Dr JF Bonaparte.

Geographic Location

This site is close to the National Route 151, which runs from Neuquén to Cerros Colorados. The locality is at the first Cretaceous outcrop next to a maintenance trail that follows the high tension line going to El Chocón.

Stratigraphic Position

Neuquén Group. Probably Anacleto Member of the Río Colorado Formation.

Age

Late Cretaceous, pre-Maastrichtian Senonian.

Lithology

Dark reddish brown siltstones.

Faunal List of the Locality

Sauropoda

Titanosauridae indet

Theropoda

Coelurosauria? indet.

Crocodylia indet.

e. Medanitos, Catriel area, Río Negro Province

History

Mr Roberto Abel discovered titanosaurid bones in 1984. The material is housed at the Museo Provincial 'Carlos Ameghino' of Cipolletti, Río Negro Province.

Geographic Location

The area is located 15 km south of Catriel, by route 151 (Abel, pers. comm.).

Stratigraphic Position

Probably Río Colorado Formation, according to the geological maps of Uliana and Dellapé (1981).

Age

Late Cretaceous, pre-Maastrichtian Senonian (Digregorio & Uliana 1980), Campanian (Uliana & Dellapé 1981).

Lithology

Friable grey sandstones (Abel, pers., comm.)

Faunal List of the Locality

Sauropoda

Titanosauridae

Neuquensaurus sp

Titanosaurus sp.

Faunal List of the Locality

Sauropoda

Titanosauridae

Neuquensaurus sp. (n. gen.?)

Titanosaurus araukanicus (Huene)

Pellegrinisaurus powelli Salgado 1996

Titanosauridae indet.

Theropoda

Abelisauridae

Abelisaurus comahuensis Bonaparte
and Novas 1985

Carnosauria indet.

Crocodylia indet.

Chelonia indet.

Plesiosauria

Pliosauroidae

Trinacromerum lafquenianum

Gasparini and Goffi in Casamiquela
(1984).

These remains were found in the same area but in an Upper Member (Andreis et al. 1974).

f. Lago Pellegrini, Río Negro Province (Map 4)

History

The area of Lago Pellegrini, situated close to the locality of Cinco Saltos, provided important fossil remains from the sandstones of the Allen Formation. Most of these findings are related to the activity of small quarries in which the friable levels of sandstone are extracted. Professor Roberto Abel, of the Museo 'Carlos Ameghino' de Cipolletti, collected numerous teeth of dinosaurs (sauropod and theropods), crocodiles, and fragmentary bones referable to sauropods, crocodiles, turtles, birds and fish. In 1975 Professor Abel began excavations in the same zone, where he found remains of titanosaurids in the quarry of Mr Pedro Cral, known as the 'Cantera de la Pala Mecánica'.

He found remains of an incomplete but articulated skeleton of a titanosaurid. This material was studied by Powell (1986) and formally described as *Pellegrinisaurus powelli* by Salgado (1996). The holotype of the theropod *Abelisaurus comahuensis* (Bonaparte & Novas 1985) also comes from this locality.

Geographic location

Several fossiliferous sites are located close to the southern shore of the Lago Pellegrini.

Stratigraphic position

Allen Formation, Malargüe Group (Andreis et al. 1974).

Age

Late Cretaceous, early Maastrichtian. For additional details see the above data about the Cinco Saltos locality.

Lithology

The Lower Member of Allen Formation is characterised by medium to coarse light yellowish friable sandstones.

g. General Roca, Río Negro Province (Map 5)

History

This locality has special historical significance, as it constitutes the leading site with dinosaur remains. The first reference of the discovery of fossil bones of large size was made by Doering (1882) when he alluded to, '... a fragment of gigantic bone and other different things originating on the first lower terrace ...' on the south bank of the Río Negro, near Fresno Menocó. These specimens were given to Captain Jorge Rohde one year later. He probably encountered them during the campaign of the General Roca in the Desert, carried out in 1879. Although these specimens were not identified specifically as dinosaurs, they presumably were because geographic, geomorphologic and lithologic data presented by Doering, suggest this same area, and that these remains come from the Late Cretaceous. The same Rohde gave to Florentino Ameghino various boxes that contained part of the fossils found at 'Fuerte Roca'. 'Among this material were some pieces of a gigantic dinosaur,' there were also some bones of crocodiles who had concavoconvex vertebrae assumed to belong to 'the extinct family Opisthocoelids' (Ameghino, 1885). In 1912 Dr R Wichmann took a trip to this area and found a specimen on the south bank of the Río Negro, and gave to General Roca 'numerous bones of a dinosaur represented by a cranium, bones of the limbs, vertebrae and ribs.' Numerous specimens were found later (Wichmann 1916).

The major part of these specimens were taken to the collections of the Director General of Mines at the Museo Argentino de Ciencias Naturales 'B Rivadavia' and studied by Huene (1929a) in his monograph.

Geographical Location

The area which provided the specimens found by Wichmann (1916) is located close to the right bank of the Río Negro, 15 km to the south-west of the city of General Roca, El Cuy Department, Río Negro Province. Access to this area is by the route that goes from General Roca to El Cuy, it is located 4.5 km to the west of the only bridge over the Río Negro. It is in an area of extensive erosion on the first terrace of the river, with abundant outcrops that make the relief typical of 'badlands'.

Stratigraphic Position

Río Colorado Formation. Anacleto Member? Neuquén Group. Bonaparte and Gasparini, (1979).

Age

Late Cretaceous, pre-Maastrichtian Senonian (Digregorio & Uliana 1980). Campanian? (Uliana & Dellapé 1981).

Lithology

The level which contains the fossils found by Wichmann, was relocated on the basis of the photographs of the locality included in Wichmann (1916, p. 259). Most specimens were found in a bank of very light grey, fine sandstone with light grey and pink patches, 2.3 m thick. The beds are laterally continuous and uniform. In the outcrop in this place are various small layers with the characteristics mentioned above, alternating with layers of coarse reddish brown, dark carbonate concretions which are abundant and thick in the lower part.

Faunal List of the Locality

Sauropoda
 Titanosauridae
 Antarctosaurus wichmannianus
 Huene 1929a
 Titanosauridae
 Titanosaurus sp. Lydekker
Chelonia indet.
Gastropoda indet.

h. Rancho de Avila, Cerro Policía, Río Negro Province

History

This locality was worked by Roth and Schiller of the Museo de La Plata during 1921 and 1923. The material obtained in this region appears to have been found at different points according to the information offered by Huene (1929a).

Geographic Location

The outcrop is located in the El Cuy Department, Río Negro Province, accessed by Route 241 which joins Neuquén with El Cuy, 80 km from Neuquén. According to Huene (1929a), the bed is located at a level situated about 30 m below the top of the canyon 'on the northern edge of the highest plateau', which is, of course, situated between Jagüelitos and Cerro Policía, 8 km to the east of the latter site.

Age

Neuquén Group. No actual information has been obtained about the stratigraphical level from which these specimens were obtained.

Lithology

Light sandstones with multi-coloured marls similar to those of Aguada del Caño (Huene 1929a).

Faunal List of the Locality

Sauropoda
 Titanosauridae
 Titanosaurus sp. Lydekker
 Titanosauridae indet.

i. Salitral Moreno, Río Negro Province

History

The first data regarding the presence of fossils at this site was communicated to the author of this work by Professor Roberto Abel in 1983, at that time Director of the Museo Provincial 'Carlos Ameghino'. Excavations began in 1984, when titanosaurid and hadrosaurid remains were found with numerous isolated bone fragments of turtles and eggshells. In addition the remains of plant fossils consisting of abundant stems and fruits, probably corresponding to araucariaceans (Powell 1987) were found in association with hadrosaurs. Recently, Salgado and Coria (1996) reported the evidence of an ankylosaur found at this locality.

Geographic Location

The site of Salitral Moreno is 20 km south of General Roca situated on the south-east margin of the Salitral Morcno depression.

Stratigraphic Position

Allen Formation, Malargüe Group.

Age

Early Maastrichtian (based on the same evidence put forward above to date the Cinco Saltos and Lago Pelleginini localities).

Lithology

Medium to coarse yellowish and greenish-grey fluvial sandstones, poorly sorted. One of the sites is a conglomeratic sandstone in which the conglomerate clasts are fossil bones. The fossils at this particular site consist predominantly of vertebrae together with frequent cranial material of hadrosaurs and juvenile titanosaurs.

Faunal List of the Locality

Sauropoda

Titanosauridae

Aeolosaurus sp.

Titanosauridae indet.

Theropoda indet.

(remains of bones, teeth, and eggs)

Ornithopoda

Hadrosauridae

Lambeosaurinae indet. (Powell 1987)

Ankylosauria indet. (Salgado & Coria 1996)

Chelonina indet.

Gastropoda indet.

j. Salina Trapalco, Río Negro Province

History

The only specimens known from this locality were discovered by Professor Roberto Abel. They are deposited in the collections of the Museo Provincial 'Carlos Ameghino' of Cipolletti. The material includes two dermal plates and the centrum of a dorsal vertebra.

Geographic Location

On the north border of Salina Trapalco, in the region of the Puesto Mansilla, located 60 km to the south of Villa Regina, Río Negro Province.

Stratigraphic Position

Neuquén or Malargüe Group.

Age

Probably Late Senonian.

Characteristics of the Sediments

'Greyish sediments' (Abel, pers. comm.). There is no additional data.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

4. Late Cretaceous covering of the Massif de Somón Curá

Several important sites are related to the Cretaceous deposits covering the Massif de Somón Curá, situated between the Neuquina, Cikiradi and San Jorge basins. These sequences are relatively thin and correspond to the Late Senonian (Campanian?–Maastrichtian). These levels represent an extension of the basins mentioned above in the last third of the Late Cretaceous.

a. Mina Antonio Mellado, Río Negro Province (Map 7)

History

A collection was given in 1952 to the Museo Argentino de Ciencias Naturales 'B Rivadavia' including parts of a long bone identified as MACN 17494; these were donated by Mr René Casamiquela.

Geographic Location

Approximately 1000 m from the diatomite mine of A. Mellado, situated 80 km north of Ingeniero Jacobacci, close to Cerro Mesa, in the area of Carri Laufquen Grande.

Provisional Stratigraphy

According to Coria (1979), the fossiliferous level corresponds to Angostura Colorada Formation (Volkheimer 1973) or Coli Toro Formation (Bertels 1969).

Age

Late Cretaceous, Senonian probably Campanian–Maastrichtian.

Lithology

No data available.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

b. Ingeniero Jacobacci, Río Negro Province (Map 7)

History

This site was located by Dr Rodolfo Casamiquela. The excavation was conducted by him and Dr Ph. Taquet, who collected articulated specimens of at least four hadrosaurs and an incomplete juvenile titanosaurid (Casamiquela 1978; 1980).

Geographic Location

This formation is situated 3 km to the north of Ingeniero Jacobacci, on the northern slope of a gentle rise oriented east–west ending to the north in the Cañadón Hahuel.

Stratigraphic Position

Coli Toro Formation (*sensu* Coria 1979).

Age

Campanian?–Maastrichtian

Characteristics of the Sediments

This unit is characterised by sands and yellowish limonite, interpreted by Casamiquela (1980) as lake deposits.

Faunal List of the Locality

Casamiquela (1980) listed the following taxa:

Ornithopoda

Hadrosauridae

Hadrosaurinae indet.

Sauropoda

Titanosauridae

c. La Calera or Bajo Colorado, Río Negro Province (Map 7)

History

The material found at this site was donated by Mr René Casamiquela to the Museo Argentina de Ciencias Naturales 'B Rivadavia' in 1952.

Geographic Location

The site is located 5 km north of the locality of Ingeniero Jacobacci, Río Negro Province.

Stratigraphic Position

Probably Angostura Colorado Formation.

Age

Late Cretaceous, Senonian, possibly Campanian.

Lithology

No data available.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

d. Los Menucos, Río Negro Province

History

Bones of large titanosaurs of this locality are deposited in the collections of the Museo de La Plata. The material was obtained from Mr Alejo Barrios of Choele-Choele, Río Negro Province.

Geographic Location

Los Menucos, Río Negro Province. No additional data available.

Stratigraphic Position

Possibly Angostura Colorado Formation. There are Late Cretaceous units in this area (Lapido et al. 1984).

Age

Late Cretaceous, Senonian, possibly Campanian.

Lithology

No data available.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

e. Estancia Los Alamitos, Río Negro Province

History

In 1982 Dr JF Bonaparte, with personnel of the Museo de Ciencias Naturales 'B Rivadavia' and the Fundación Miguel Lillo de Tucumán, discovered Cretaceous reptiles at this site. The work in this area was prompted by information provided earlier by the geologists Eliseo Sepúlveda and Mario Franchi of the Servicio Geológico Nacional.

Dr Bonaparte and his team continued the prospecting with special attention to the microvertebrates during 1983–85. As a result of this work, he obtained an important collection of vertebrates that included mammals, dinosaurs, hadrosaurs, titanosaurs, theropods, turtles, lizards, snakes, frogs, and fish. Hadrosaurs and mammals were used to support the connection of North and South America during the Late Cretaceous (Bonaparte 1984a, b, c; 1996; Bonaparte et al. 1984).

Geographic Location

The formation is exposed in the area of the Arroyo Verde, above the south-west slopes of Cerro Cuadrado, within the borders of the Estancia 'Los Alamitos'. This place is situated 40 km to the south-east of the Cona Niyeu, Río Negro Province.

Stratigraphic Position

Lower section of the Los Alamitos Formation (Franchi & Sepúlveda 1983).

Age

Late Cretaceous, Campanian or probably Early Maastrichtian (Bonaparte 1984a).

Lithology

Fluvial yellow and yellowish-green sandstones and siltstones. The level carrying the remains of titanosaurs is composed of yellowish siltstones.

Faunal List of the Locality

Osteichthyes

Holostei indet.

Dipnoi

cf. *Ceratodus* sp.

Amphibia

Anura indet.

Ophidia indet.

Lacertilia indet.

Chelonina—three genera indet.

Ornithopoda

Hadrosauridae

Hadrosaurinae

Kritosaurus australis

Bonaparte et al. 1984

Theropoda indet.

Sauropoda

Titanosauridae

Aeolosaurus rionegrinus?
n. gen. et n. sp.

Mammalia

Mesungulatum housayi
Bonaparte and Soria 1985
Austroriconodon sepulvedai
Bonaparte 1992
Ferugliotherium windhausenii
Bonaparte 1986
'Vucetichia gracilis'
Bonaparte 1990
Bondesius ferox
Bonaparte 1990
Groebertherium stipanicici
Bonaparte 1986a
Groebertherium novasi
Bonaparte 1986a
Leonardus cuspidatus
Bonaparte 1990
Reigitherium bunodonta
Bonaparte 1990
Brandonia intermedia
Bonaparte 1990
Casamiquelia rionegrina
Bonaparte 1990
Barberenia araujoae
Bonaparte 1990
Quirogatherium major
Bonaparte 1990

5. San Jorge Basin

This basin has a thick sequence of Cretaceous sediments with abundant remains of dinosaurs (mainly sauropods) which have been known for a long time as *Argyrosaurus superbus* Lydekker. The most important formations are exposed in the area of the Sierra San Bernardo, near the bend of the Río Senguerr and close to the banks of the Río Chico.

a. East of the Río Chico, Chubut Province

History

An expedition of the Museo de La Plata excavated a hind limb of a large sauropod found by Carlos Ameghino earlier (Ameghino 1898). According to this author, the remains belong to an almost complete skeleton. Fragments of the rest of the skeleton were left at the site. A femur of a large Titanosaurid was collected not far from that site on an expedition directed by Dr JF Bonaparte in 1980.

Geographic Location

Lydekker (1893) mentioned that the type of *Argyrosaurus superbus* came from the Río Chubut. However, Huene (1929a) indicated that it came from the left bank of the Río Chico, near to the Pampa Pelada to the north-east of Lago Colhué Huapi, in the Province of Chubut. Huene checked it personally with Carlos Ameghino.

Nevertheless, Florentino Ameghino (1898) placed the site, '... en el águila que forma el Río Chico con el Lago Musters ...' 'en el águila que forma el Río Chico con el Lago Musters' (in the angle between the Río Chico and Lago Musters) which seems to coincide with what was discovered by Riggs, located now in the Estancia 'La Angostura', on the south bank of Río Chico (Marshall 1978).

Stratigraphic Position

Bajo Barreal Formation, Chubut Group (Bonaparte & Gasparini 1979). According to Huene (1929a) the type of *Argyrosaurus superbus* was taken from a level 100 m beneath the 'layers with *Notostylops*'.

Age

Late Cretaceous. The age of the Chubut Group has been the object of diverse interpretations. Lesta and Ferello (1972) and Lesta, Ferello and Chebli (1980) have proposed a Valanginian–Early Senonian age. Romero and Argüjo (1981) postulated an Aptian–Turonian age based on paleobotanical evidence found in the Castillo Formation. Bonaparte and Gasparini (1979) on the other hand, suggested that the evidence provided by the sauropod dinosaurs confirms the Senonian age proposed by Huene (1929a).

The revision of the Titanosaurid family presented in this work, and biostratigraphic considerations that are presented later (Chapters 5, 8 and 9) allow the inference of a Late Cretaceous age. The characteristics of *Campylodoniscus ameghinoi* supports the hypothesis of Romero and Argüjo (1981), who admitted the possibility of an older age (pre-Campanian?) in the Late Cretaceous.

Lithology

No data available.

Faunal List of the Locality

Sauropoda

* Titanosauridae

Argyrosaurus superbus Lydekker, 1893

b. Bend of Río Senguerr, Chubut Province (Map 9)

History

The first indication of dinosaur remains in this area was offered by Mr Pablo Baltuska, owner of the land. Part of the specimens coming from this locality were obtained in 1976 by an expedition of the Fundación Miguel Lillo and the Facultad de Ciencias Naturales de la Universidad

Nacional de Tucumán, directed by Dr JF Bonaparte. Excavations were completed later by Bonaparte, collecting for the Museo de Ciencias Naturales 'B Rivadavia'.

Geographic Location

On the right bank of the Río Senguerr, on the northern border of Pampa María Santísima, Sarmiento Department, Chubut Province.

Stratigraphic Position

The lower part of the Laguna Palacios Formation (Bonaparte 1978; Bonaparte & Gasparini 1979). Sciutto (1981) instead concluded that it corresponds to Bajo Barreal Formation, Chubut Group.

Age

Late Cretaceous on the basis of the same considerations that have been presented for the Pampa Pelada locality.

Characteristics of the Sediments

Yellow sandstones.

Faunal List of the Locality

Sauropoda

Titanosauridae

Argyrosaurus superbis? Lydekker, 1893

Carnosauria indet.

c. Estancia Ocho Hermanos, Chubut Province

(Map 10)

History

The first discovery of fossils was made by Dr JC Sciutto, of the petroleum company YPF. In 1979, a team from YPF and the Fundación Miguel Lillo found Cretaceous vertebrates in the area including remains of sauropods, carnosaurs and turtles. In 1981 Dr JF Bonaparte and his team discovered an articulated series of dorsal and sacral vertebrae of a big sauropod at the Estancia 'Ocho Hermanos'. However, that material was not extracted during that field trip and a cast of it was prepared, later used as a paraplotype of *Epachthosaurus sciuttoi*. The original was excavated several years later by personnel of the Universidad de la Patagonia 'San Juan Bosco'. Later, Prof. Rubén Martínez and his team found an articulated specimen referred to that species (Martínez et al. 1989).

Geographic Location

Estancia 'Ocho Hermanos' facing Bajo Guadaloso, in the Sierra de San Bernardo, Sarmiento Department, Chubut Province.

Stratigraphic Position

Bajo Barreal Formation, Chubut Group, (Sciutto 1981).

Age

Late Cretaceous. An unusual association of primitive titanosaurs and non-titanosaurid dinosaurs with

amphicoelous caudal centra suggests a Late Cretaceous but pre-Senonian age for the Bajo Barreal Formation at this locality (Powell et al. 1989).

Lithology

Light greenish-grey quartz sandstones.

Faunal List of the Locality

Sauropoda

Titanosauridae

Epachthosaurus sciuttoi Powell 1990

Sauropoda indet.

Theropoda

Xenotarsosaurus bonapartei Martínez et al. 1986

Chelonia

Pelomedusidae indet.

d. Sierra de San Bernardo

History

Several discoveries have been made at the southern end of this mountain range by palaeontologists at different times. Carlos Ameghino discovered the first specimens. Others were found by EC Riggs, in charge of an expedition of the Field Museum of Natural History, in 1924. In 1975 Bonaparte and his team collected additional specimens. These specimens are housed in the collections of Paleontología Vertebrados Lillo and consist of a large femur and a caudal vertebra found on the Estancia Silinis, and a large tibia coming from an outcrop close to the bend of the Río Senguerr.

Geographic Location

Several sites situated mainly on the eastern side of the southern end of the Sierra de San Bernardo, Chubut Province.

Stratigraphic Position

Castillo and Bajo Barreal Formations (Chubut Group).

Age

Late Cretaceous

Lithology

No registered data

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

c. Western Slope of the Sierra de San Bernardo

The only data related to the geographic provenance of *Campylodon ameghinoi*, discovered by Carlos Ameghino, were given by Huene (1929a). He stated 'On the West edge of the Sierra de San Bernardo, West of Lago Musters'. The stratigraphic level which it came

from is also imprecise, indicated just as 'variegated sandstones'. This certainly corresponds to units of the Chubut Group.

The specimen of *Campylodoniscus ameghinoi* consists of an incomplete maxillary that will be described later.

6. Austral Basin

This basin is predominately made up of marine sediments. This sequence represents almost all of the Cretaceous (Malumián et al. 1983) with some continental episodes suggested by the sediments of the Mata Amarilla Formation (in part), Chorrillo and Cardiel Formations.

a. Río Leona, Santa Cruz Province

History

Some caudal vertebrae were found in the area. The material is housed in the collections of the Museo Argentino de Ciencias Naturales 'B Rivadavia'. The specimens were donated by Mr Teodoro Caillet-Bois in 1918 (Huene 1929a).

Geographic Location

According to Carlos Ameghino (Huene 1929a), the specimens came from an area near Lago Argentino situated on the left bank of Río Leona, Lago Argentino Department, Santa Cruz Province.

Stratigraphic Position

Chorrillo Formation (Feruglio 1949).

Age

Late Cretaceous, Maastrichtian (Furque 1973). The Chorrillo Formation lies conformably on the marine sediments of the Anita Formation. The Chorrillo Formation is assigned to the Campanian by Leanza (1967) based on its fossils and to the Campanian–Early Maastrichtian by Furque (1973). The deposits which yielded titanosaurs are covered by another marine unit, the Calafate Formation, whose age based on fossils is Late Maastrichtian (Furque 1973).

Lithology

There is no data in the literature about the sediments in which the caudal vertebrae were found. According to the studies of Feruglio (1938), the levels with dinosaur bones in the valley of the Río Leona, consist of 'grey and greenish grey clays, with dark and purple bands alternating with generally friable beds. In this part no marine fossils were found, but there are frequent logs of petrified wood and dinosaur bones'.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

b. Lago Argentino, Santa Cruz Province (Map 11)

History

Recently, Dr JF Bonaparte, of the Museo Argentino de Ciencias Naturales 'B Rivadavia', collected and studied some specimens of large titanosaurs located by General F Nullo in the Estancia 'Anita' (Bonaparte, pers. comm.).

Geographic Location

Lago Argentino, Santa Cruz Province

Stratigraphic Position

Chorrillo Formation (Feruglio 1949)

Age

Late Cretaceous, Maastrichtian (Furque 1973).

Lithology

These are considered to be the same as the outcrops at the Río Leona locality.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

Theropoda indet.

c. Lago Cardiel, Santa Cruz Province

History

There is only one specimen from this locality placed in 1925 in the collections of the Museo Argentino de Ciencias Naturales 'B Rivadavia', donated by Mr Domingo Pasolini. Piatnitzky (1938) and Ramos (1982) cited the presence of dinosaurs on the Península de Las Tunas and other points in Estancia 'Las Tunas'.

Geographic Location

Lago Cardiel, Santa Cruz Province.

Stratigraphic Position

Probably Cardiel Formation (Ramos 1982).

Age

Late Cretaceous. There are various hypotheses concerning the age of the Cardiel Formation. Ramos (1982) suggested that it is post-Albian in age. This interpretation agrees with Russo et al. (1980) that this unit was contemporaneous with the Mata Amarilla Formation dated as Coniacian based on ammonites. According to Russo et al. (1980), regional considerations indicate a Maastrichtian age for the Cardiel Formation.

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

d. Río Sehuen, Santa Cruz Province**History**

Carlos Ameghino discovered some remains of dinosaurs which were studied by his brother Florentino (Ameghino, 1898) and named *Loncosaurus argentinus* and *Clasmodosaurus spatula*. The later species, based on some incomplete teeth, was originally interpreted as a sauropod, and later considered both sauropod (Huene 1929a, pp. 17, 140) and coelurosaurid (Huene 1929a, p. 141). Bonaparte (1978) concurred with Huene's last mentioned opinion. In this work *Clasmodosaurus spatula* is reinterpreted as titanosaurid (see Chapter 5).

Geographic Location

Western slope of the southern tributary of the Río Sehuen, 50 km east of Lago Viedma and 30 km south of Mata Amarilla (Huene 1929a).

Stratigraphic Position

Probably Cardiel Formation

Age

Late Cretaceous, Maastrichtian

Faunal List of the Locality

Theropoda

Coelurosauria

Loncosaurus argentinus

Ameghino 1898

Sauropoda

Titanosauridae

Clasmodosaurus spatula

Ameghino 1898 *nomen dubium*

B. BRAZIL**1. Basin of the Baurú Formation (Map 1)**

The area where the sediments of the Baurú Formation were deposited was named Baurú Basin by Malumián et al. (1983, Fig. 7). It is part of the Paraná sub-basin, included in the vast intracratonic Chaco-Paraná Basin. It extends through the states of São Paulo, Minas Gerais, Goiás, Mato Grosso, Mato Grosso do Sul and Paraná, also reaching into north-western Paraguay (Suguio & Barcelos 1983).

The first fossil specimens were made known by von Ihering (1911) from the locality at São Jose do Rio Preto (see below for description of this locality). Later, many discoveries were made in the Baurú Formation. The profuse record of fossils includes vegetation (algae), invertebrates, (molluscs and crustaceans), and vertebrates (fish, turtles, titanosaurid and theropod dinosaurs). Mezzalana (1980) published a list of the fossils found in the Baurú Formation.

a. São Jose do Rio Preto, State of São Paulo (Map 12)**History**

Von Ihering (1911) studied the fossils obtained from this locality. The discovery of these specimens was made two years earlier in a cistern, on the property of Father RA Purita. Von Ihering (1911) identified among these specimens a tooth of a dinosaur, fragments of turtle plates, teeth of crocodiles and shells of molluscs, characterising for the first time the Baurú Formation from a palaeontological point of view.

Arid and Vizotto (1971) described the titanosaurid *Antartcosaurus brasiliensis*, found close to São Jose do Rio Preto. The discovery was made during operations related to the widening, drainage and paving of the roadway between São Jose do Rio Preto and Barretos. However, the fragmentary nature of this specimen, and the lack of diagnostic features prevent a precise identification. Consequently, it is considered here as Titanosauridae indet.

Geographic Location

State Road São Jose do Preto-Barretos, 5 km from the original locality situated in the north-west of the State of São Paulo.

Stratigraphic Position

Baurú Formation

Age

Late Cretaceous Senonian (Huene 1939 in Oliveira & Leonards 1978).

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

Chelonia indet.

Crocodylia indet.

Gastropoda

Basommatophora

Physa arida Mezzalana 1974

b. Peirópolis, State of Minas Gerais (Map 13)**History**

The existence of fossil vertebrates at this locality was communicated to the Departamento Nacional do Produção Mineral, by Dr JF Junior of the Instituto Geográfico y Geológico in 1947. Much later, a group of geologists made up of KE Caster, FPM de Almeida, O Barbosa, and S Petri found bone fragments in the same area.

Excavation began in 1947–48, under the direction of Dr LL I Price, continuing intermittently for many years. All of the specimens collected by Price are housed at the museum of the Departamento Nacional do Produção Mineral of Rio de Janeiro.

The collected specimens came from seven different locations close to the Peirópolis Station of the Railroad Mogiana, 19 km to the east of Uberaba, State of Minas Gerais, Brazil (Price 1955).

Stratigraphic Position

In lower and middle part of the Baurú Formation (Baurú member or facies).

Age

Late Cretaceous, Senonian (Huene 1939 in De Oliveira & Leonardos 1978).

Lithology

Coarse light yellowish-grey argillaceous sandstones. The deposits are considered to represent a fluvial environment because of the presence of rounded clasts marking the stratification (Price 1955).

Faunal List of the Locality

Sauropoda

 Titanosauridae

 cf. *Titanosaurus* sp. (this work, Chapter 5)

 Titanosauridae indet. (this work, Chapter 5)

Carnosauria indet.

Coelosauria indet.

Crocodylia

 Mesosuchia

Peirosaurus torminni Price 1955

Peirosaurus torminni was found in a different lithotype from the rest of the fossils, but at the same level. It was in a fine yellowish sandstone and claystone with the remains of gastropods and poorly preserved plants. According to Price (1955) this lens corresponds to a flood deposit, or a marginal deposit by the withdrawal of the river (an oxbow). This lens was unexpectedly found in the fluvial deposits which make up most of the formation. Infraorder indet.

Itasuchus jesuinoi Price 1955

Anura

 Neobatrachia

 Leptodactylidae

Teleostei indet.

c. Campina Verde, State of Minas Gerais

History

There is no data. The specimens are housed at the Museum del Departamento Nacional do Produção Mineral of Rfo de Janeiro.

Geographic Location

This area is situated to the north of the locality with the same name, in the western part of the State of Minas Gerais.

Stratigraphic Position

Baurú Formation.

Age

Late Cretaceous, Senonian (Huene 1939 in De Oliveira & Leonardos 1978).

Lithology

No available data.

Faunal List of the Locality

Titanosauridae indet.

d. Mangabeira, State of Minas Gerais

History

This is the first locality where dinosaurs were found in the State of Minas Gerais. The presence of fossil remains in this area was communicated by Engineer L Feijó Bittencourt in 1945 to D. G. M. of the Departamento Nacional Produção Mineral. The discovery was related to the work that was being done to relocate the Ferrocarril Mogiana, for which large quantities of crushed rock were needed (Price 1951).

Geographic Location

Mangabeira is about 1 km to the north of Uberaba, in what is called 'Triângulo Mineiro', situated in the eastern part of the state of Minas Gerais.

Stratigraphic Position

Baurú Formation (Price 1951).

Age

Late Cretaceous, Senonian (Huene 1939 in De Oliveiras & Leonardos 1978).

Faunal List of the Locality

Sauropoda

 Titanosauridae indet.

e. Ibirá, State of São Paulo (Map 12)

History

The discovery was made by Mr Henrique Orlando, owner of the 'Fazenda São Vincente', and consists of some fragments of bones and teeth, which indicated evidence of transport. Arid and Vizzoto (1973) have reviewed the geologic characteristics of the fossiliferous levels, indicating the fossils identified in this site.

Geographic Location

'Fazenda São Vincente', is 10 km from the Municipality of Ibirá, state of São Paulo.

Stratigraphic Position

Upper member of the Baurú Formation.

Age

Late Cretaceous, Senonian (Huene 1939 in De Oliveira & Leonardos 1978).

Lithology

Light calcareous sandstones, lenticular, with beds of variable thickness from 0.2 m to 1 m. Arid and Vizzoto (1973) said that the lithotype is characteristic of a flood plain, typical of the Baurú Formation.

Faunal List of the Locality**Sauropoda**

Titanosauridae indet.

Theropoda indet.

Chelonía

Pelomedusidae

Podocnemis sp.? Price

Crocodylia

Goniopholidae? Price

Osteichthyes indet.

f. Guararapes, State of São Paulo (Map 12)**History**

The discovery was made at the 'Fazenda Ríó Preto' and collected in 1970 during the excavation for a concrete well. The specimens were kept by Messrs A. De Sales and R. Berry, the administrators of this establishment, and made available for study later (Leonardi & Duszczac 1977).

Geographic Location

Fazenda Ríó Preto, near Património, located 12 km to the south of Guararapes, state of São Paulo.

Stratigraphic Position

Baurú Formation, 100 m above the level of the underlying basalts.

Age

Late Cretaceous, Senonian (Huene 1939 in De Oliveira & Leonardos 1978).

Lithology

Bright red sandstones.

Faunal List of the Locality**Sauropoda**

Titanosauridae indet.

(Leonardi & Duszczac 1977).

g. Pacaembú Paulista, State of São Paulo (Map 12)**History**

As a result of the operations of the Companhia Paulista do Ferrocarriles, numerous invertebrate and vertebrate fossil discoveries were made in various levels of the Baurú Formation. The new outcrops were revealed in cuts, and prospected by Dr S Mezzalira who published a summary of the findings (Mezzalira 1959).

Geographic Location

Cut Number 45, km 15 (the cuts are numbered from Adamantina to Paulicea) Municipality of Pacaembú Paulista, in the western part of the state of São Paulo.

Stratigraphic Position

Baurú Formation (Mezzalira 1959).

Age

Late Cretaceous, Senonian (Huene 1939 in De Oliveira & Leonardos 1978).

Lithology

No available data.

Faunal List of the Locality**Sauropoda**

Titanosauridae indet.

C. URUGUAY (Map 14)

There is an important lack of precise data about the history and characteristics of several localities with dinosaurs in Uruguay. For this reason they will not be considered in detail. The sites are located in the area of Cretaceous sedimentation, which is known in this work as Guichón-Ycruá (Malumián et al. 1983), mentioned when discussing the locality of Calera Barquin, Entre Ríos, Argentina.

History

The first discoveries in this country were made by Mr Alejandro C Berro. He made an important collection of vertebrate fossils, which are housed now at the Museo Paleontológico 'AC Berro' in Castillo Mauá, managed by the Intendencia Municipal de Soriano, Mercedes, Soriano Department, Uruguay. Other specimens, mostly found by occasional collectors, belong to the collections of the Museo Nacional de Historia Natural de Montevideo.

Some specimens were studied by Huene (1931) during a visit to Uruguay. He assigned them to previously described species of titanosaurs from Patagonia as *Neuquensaurus australis* (= *Titanosaurus australis sensu* Huene), *Titanosaurus araukanicus* (= *Laplatasaurus araukanicus sensu* Huene), *Antarctosaurus giganteus* and *Argyrosaurus superbus*. The taxa are usually referred to in later geologic papers.

Geographic Location

The localities identified with an asterisk have been taken from Rusconi (1932). The rest were obtained from the catalogues of the Museo de Historia Natural de Montevideo and the Museo Paleontológico 'AC Berro'.

Soriano Department: Arroyo La Lancha y Maciel, 10 km to the north of Rodó*, Arroyo El Aguila, and Arroyo Los Laureles*, Arroyo Ascencio, in the place known as El Grito de Ascencio, in the Estancia 'Morixe'.

Río Negro Department: Arroyo Mbopicuá*; Estancia 'Nueva Mehlem', facing opposite Mercedes; Campo El Cambará, near Colonia San Javier.

Paysandú Department: Guichón; Arroyo Nacurutú; Arroyo Gutierrez Chico and Grande* (Ubilla pers. comm.).

Durazno Department: Arroyo Los Perros; Molles.

Canelones Department: Arroyo Piedra Sola.

Colonia Department: Arroyo Tala de Miguelete, 12 Sección Policial, ranch of Mr Luis Morquio (Mones 1980).

Stratigraphic Position

According to Bossi et al. (1975) the dinosaur remains are usually found in the sediments of the Asencio Formation.

Age

Huene (1929b, 1931) has inferred a Late Senonian age, the reason was the associations that were identified as corresponding with those of that age in Patagonia, Argentina.

In light of more detailed observations, the specimens listed from Uruguay are not good enough to identify at the generic or specific level. They are thus of little use in correlation. It is therefore considered prudent, at this time, to regard these fossils as Late Cretaceous in age.

Lithology

The precise stratigraphic levels of the Uruguayan specimens are not known, as usually we are dealing with eroded specimens found in the bed of arroyos. The Asencio Formation is characterised by pinkish and whitish fine sandstones with calcareous or argillaceous cement.

The dinosaur fossils have two types of preservation: (1) bone completely replaced by silica, and (2) cells of the spongy tissue filled with quartz.

Faunal List of the Locality

The specimens obtained in Uruguay were identified by Huene (1929a, 1931), based on isolated and incomplete specimens, which belonged to the species *Neuquensaurus australis* (= *Titanosaurus australis*), *Titanosaurus araukanicus* (= *Laplatasaurus araukanicus*), *Antarctosaurus wichmannianus* and *Argyrosaurus superbus*.

Nevertheless, the examination of the collections of the Museo 'AC Berro' and the Museo Nacional de Historia Natural de Montevideo, revealed the impossibility for this author to refer the fossils to the species or generic level, because the collections mostly consist of fragmentary specimens that are not useful for precise identification.

Documented Fauna

The studies done in this work are limited to this list only. Sauropoda

Titanosauridae

Titanosauridae indet.

To this list might be added the parataxa *Sphaerovum erbeni* based on eggs referred to titanosaurids described by Mones (1980) (Pl. 65:1–4).

D. CHILE

1. Andina Basin

a. Pichasca, Coquimbo Province (Map 15)

History

The existence of fossil bones was detected by Miss Irene Tapia, of the Instituto de Investigaciones Geológicas de Chile. Dr Rodolfo Casamiquela excavated additional specimens of dinosaurs and chelonians. An account of the geology and palaeontology of the site was published by Casamiquela et al. (1969). Later Torres and Rallo (1981) and Gonzalez (1971) studied the paleobotanical specimens obtained from this formation.

Geographic Location

Area of Pichasca, 40 km to the north-east of Ovalle, Coquimbo Province, Chile.

Stratigraphic Position

Viñita Formation (Casamiquela et al. 1969).

Age

Late Cretaceous, Senonian? Aguirre and Egert (1965) tentatively estimated a Late Albian to Early Coniacian age for the Viñita Formation.

Casamiquela et al. (1969) inferred a Late Maastrichtian age for the sedimentary levels with titanosaurid remains. They correlated the Viñita Formation to the sedimentary formations with dinosaurs of Patagonia. The present knowledge and the preservation of the available material do not allow precise identifications. Radiometric dating made by Palmer et al. (1980) based on the K-Ar method indicates an age of 64.7 million years for the Viñita Formation. These authors say, nevertheless, that the sample suggested a certain alteration of secondary minerals, which could lead to errors. These data are, however, coherent with the interpretation of Casamiquela et al. (1969).

Lithology

'Dark reddish-brown sandstones, in part with crossbedding, with interbedded lenticular layers of dark reddish to dark grey shale 30 cm thick. The sandstones contain silicified trunks of various size (exceptionally 5 m in length) and some fragments of fossil bones. The shales contain fossil leaves and stems. In some places the unit has whitish and mineralised zones with oxides of copper.' (Casamiquela et al. (1969).

Faunal List of the Locality

Sauropoda

Titanosauridae indet.

Chelonina indet.

Other Palaeontological Elements

Specimens of trunks, leaves and stems studied by Torres and Rallo (1981), who offered the following list of species:

Araucarioxylon pischaqueus Torres and Rallo

Notofagoxylon pischaqueus Torres and Rallo

Mirtoxylon pischaqueus Torres and Rallo

Elaeocaroxylon pischaqueus Torres and Rallo

b. Proximity of Cerro Algarrobito, Third Region of Atacama

History

Chong Diaz (1985) referred to the discovery of titanosaurid bone fragments, which occurred during exploration for mineral deposits.

Geographic Location

According to Chong Diaz (1985), the deposit is located in the south-east corner of the Cuadrángulo Chañarillo, southern-central area of the Third Region of Atacama, Chile. It is located in an unnamed main creek about 2.5 km to the south-east of the Cerro Algarrobito (27° 59' 15" south and 70° 15' 40" west).

Stratigraphic Position

The material has been found in a calcareous-marly bed of the Hornitos Formation. This unit is made up of sandstones, mudstones, conglomerates and limestones, with intercalated andesitic flows and breccias (Chong Diaz 1985).

Age

Late Cretaceous?–Early Tertiary (Chong Diaz 1985)

E. PERÚ

Geographic Location

Fundo El Triunfo y Pongo de Rentema, in the region of the syncline of Bagua (5° 30' south – 78° 30' west) (Mourier et al. 1986).

Stratigraphic Position

'Lower Red Beds' (Mourier et al. 1986)

Age

Late Cretaceous, Late Santonian–Campanian (Mourier et al. 1986).

Faunal List of the Locality

Sauropoda

Titanosauridae ? indet.

Theropoda indet.

Mammalia

Theria indet.

V. SYSTEMATIC PALAEONTOLOGY

Order Saurischia Seeley, 1888

Suborder Sauropodomorpha Huene 1932

Family Titanosauridae Lydekker, 1885

non Romer 1956

Titanosauridae Lydekker, 1893, pp. 2–3; Huene 1929a; Huene 1956, p. 508; Lapparent and Lavocat 1955 in part, p. 827; McIntosh 1990; Upchurch 1994, 1995; Salgado 1996 in part.

Titanosaurinae Romer 1956, p. 621; Appleby et al. 1967, p. 713; Steel 1970, p. 74; Charig 1978, p. 28.

Antarctosauridae Olshevsky 1978, p. 28.

Titanosauria Bonaparte and Coria 1993; Sanz et al. 1999.

The family Titanosauridae was erected by Lydekker (1893), to include a peculiar group of sauropod dinosaurs with procoelous caudal vertebrae. They were first discovered in India and Argentina. Huene (1927, 1929a, 1956), the experienced German reptile specialist, recognised Titanosaurids as a distinct group of sauropods, and retained the rank of family as proposed by Lydekker (1885, 1893), except in one of his works (Huene 1932). However, sauropod classification is difficult owing to the existence of numerous poorly known taxa, many of which are poorly represented. As pointed out by Romer (1968), complete skeletons are rare, skulls are infrequent and numerous taxa were described on the basis of very fragmentary remains. Before recent cladistic analysis and resulting cladograms were published, several classifications were proposed, depending on the characters considered of taxonomic value. A synthesis is presented by Romer (1968) and Swinton (1970). Generally, classifications considered titanosaurs with the rank of subfamily (Romer 1956; Appleby et al. 1967; Steel 1970; Charig 1973; Bonaparte 1978). These authors placed 'Titanosaurines' in different families: Titanosauridae (Romer 1956) and Atlantosauridae (Appleby et al. 1967; Steel 1970).

In the present work, titanosaurs are considered a monophyletic group with a family rank as originally proposed by Lydekker (1893) and Huene (1929a, 1956). This is justified by traditional use, and with the aim of avoiding the creation of new names. This position is partially concordant with the classification scheme of Berman and McIntosh (1978), McIntosh (1981, 1990) and Bonaparte (1996).

Definition of the Family

Quadrupedal herbivorous dinosaurs, of medium to gigantic size. Skull with very long and recurved paroccipital processes. Cylindrical teeth with open roots, slightly spatulated when unworn, except in *Ampelosaurus*. Short basiptyergoid processes. Thirteen cervical vertebrae, probably 12 dorsals, 6 sacrals and more than 30 caudals. The opisthocoelous presacral vertebrae have cancellous structure in the centra and bulky parts of the neural arch (neural arch peduncles, ends of neurapophyses and diapophyses). Dorsal

vertebrae without hyposphene-hypapophyses except in the primitive *Epachthosaurus*. Sacrum with completely fused vertebrae. Sacral ribs with an 'I'-shaped cross section, participating in the conformation of the acetabular articular surface. First caudal biconvex or procoelous. Remaining caudals with a posterior articular condyle, with some occasional amphicoelic elements on the distal region of the tail. Neural arches joined to the anterior portion of the centrum in the middle and posterior caudals. Hemapophyses proximally open. Scapula with the glenoid articular facet oriented forward, down and inwards. Quadrangular coracoids. Sternal plates long and relatively broad, with a concave lateral margin. Fore limbs shorter than the hind limbs. Straight femur, somewhat anteroposteriorly flattened. Fibula with a marked lateral process. Astragalus relatively narrow.

Genus *Titanosaurus* Lydekker 1877

Titanosaurus Lydekker 1877, p. 38; Huene 1956, p. 509 in part; Steel 1970, p. 77 in part; White 1973, p. 153; Olshevsky 1978, p. 28 in part.
Laplatasaurus Huene 1929a, p. 84; Huene 1956, p. 510; Steel, 1970, p. 76; White 1973, p. 138; Olshevsky 1978, p. 28; McIntosh 1990, p. 395.

Type species. *Titanosaurus indicus* Lydekker 1877

Distribution. Senonian of India, South America, Madagascar and ?Europe.

Diagnosis. Medium to large titanosaurid with slender limb bones, fibula with a lateral prominent crest perpendicularly placed over the lateral tuberosity. Anterior and medial caudal vertebrae laterally compressed, much taller than wider. Caudal elements lacking cancellous structure in the centra.

Comments

Titanosaurus indicus was based on a pair of caudal vertebrae found in the lower level of the 'Sandy Limestone Formation' at the western foothills of Bara Simla Hills, Jabalpur, India.

These specimens were first reported by Falconer (1868), but a formal description was made by Lydekker (1877) and redescribed by the same author in 1879. Swinton (1947) studied material collected from the Chota Simla, near Jabalpur (India), which he assigned to *Titanosaurus indicus*. These include an incomplete left humerus, and the proximal part of the right humerus, right tibia and fibula, and also a series of caudal vertebrae. The morphology of the caudal vertebrae suggest that they belong to this genus. However, having only two caudal elements represented in the type, the reference to the species *T. indicus* should be verified in the light of new findings. Recently, Jain and Bandyopadhyay (1997) described a new species: *Titanosaurus colberti*. It is based on bones of one individual, represented by cervical, dorsal and caudal vertebrae, scapula and coracoid, humerus, ulna, pubes and ischium. It is the most complete titanosaurid taxon described from India.

Lydekker (1893) erroneously referred a series of caudal vertebrae from Neuquén to *Titanosaurus*, for which he erected the species *T. australis*. Powell (1992) proposed a new generic name for Lydekker's species: *Neuquensaurus australis* (see below).

The same author referred a humerus (MLP Ly 15—Lydekker 1893; Pl. 4, 1), a femur (MLP Ly 119—Lydekker 1893; Pl. 2, 3) and an incomplete dorsal vertebra (MLP Ly 11—Lydekker 1893, Pl. 2) to '*Titanosaurus australis*'. According to my interpretation, this material probably belongs to the genus *Titanosaurus*. Huene (1929a) revised the material studied by Lydekker (1893), following the latter's criteria about '*Titanosaurus*'. In other words, Huene recognised at the Cinco Saltos site (Río Negro Province) and Neuquén (Neuquén Province), two distinct titanosaurid genera. The characteristic laterally compressed caudal vertebrae, the atlas, and the long and slender limb bones were included by Huene (1929a) in '*Laplatasaurus araukanicus*'. Likewise, the wide and low caudal centra, and the short, robust limb bones were assigned to '*Titanosaurus australis*' and '*T. robustus*'.

An examination of the type *Titanosaurus indicus* and the material studied by Swinton (1947), revealed that this form corresponds to a titanosaurid of medium to large size with slender limbs. The fibula is distinguished by possessing the lateral tuberosity very similar to that of *Laplatasaurus araukanicus*, as well as the robustness and proportions. The caudal vertebrae of *Titanosaurus indicus* are laterally compressed, which result in a high and narrow centrum, with a narrow ventral face and very flat lateral walls latero-ventrally oriented, also similar to those of '*Laplatasaurus araukanicus*' described by Huene (1929a). As discussed below, according to the available evidence, '*Laplatasaurus*' is considered as a synonym of *Titanosaurus*.

Titanosaurus araukanicus (Huene 1929a) Plate 5: 1, 2 and 3)

Laplatasaurus araukanicus Huene 1929a, pp. 353–56, Plates 22–27; Bonaparte 1978, pp. 558–59, Fig. 267; Bonaparte and Gasparini 1979, p. 389; Powell 1980, pp. 44–46; McIntosh 1990, pp. 395–96.

Lectotype. MLP CS 1128, right tibia (Pl. 5:1a and b) and MLP CS1127, right fibula (Pl. 5:2a and b). These specimens were designated as lectotypes by Bonaparte and Gasparini (1979) and illustrated by Huene (1929a, Pl. 27:2 and 2).

Locality. Cinco Saltos, General Roca Department, Río Negro Province, Argentina.

Stratigraphic position. Lower member of the Allen Formation (Malargüe Group).

Age. Late Cretaceous, early Maastrichtian.

Hypodigm. In addition to the lectotypes, MLP CS 1316

(cervical vertebrae); MLP CS 1145/1131/1136/1146 (dorsal vertebrae); MLP CS 1348/1315/1352, MPCA 1501 (caudal vertebrae); MLP CS 1322 (left sternal plate); MLP 1031 (right scapula); MLP CS 1262 (coracoids); MLP CS 1174 (left incomplete humerus); MLP CS 1299 (left radius); MLP CS 1299 (left radius); MLP CS 1174 (juvenile radius); MLP CS 1170/1168/1192/1196 (metacarpals); MLP CS 1059 (left pubis); MLP CS 2202/2217 (incomplete metatarsals); MLP CS 2002/1217 (incomplete metatarsals).

Diagnosis. Slender tibia, with cnemial crest longer than in *Antarctosaurus*, separated from the axis of the proximal end by a clear depression on the lateral face. Transversely wide distal end. Robustness index = 0.40. Slender fibula with prominent double lateral tuberosities, with a clearly defined depression on the anteroproximal corner of the external face.

Description

Axial skeleton

Only one cervical has been referred to the species by Huene (1929a). According to this author, it corresponds to the 8th, 9th or 10th cervical, characterised by being relatively much longer than the equivalent in *Neuquensaurus australis*. The dorsals are only represented by the centrum of a juvenile anterior dorsal vertebra (MLP CS 1145/1136).

The caudal vertebral centra are relatively short and high, with a narrow ventral moiety. The lateral walls are slightly concave, and face lateroventrally. The ventral face is narrow and it is laterally limited by edges, more prominent towards the articular facets of the hemapophyses. The first caudal of *Titanosaurus araukanicus* is not known. However, material referred to the genus shows a biconvex centrum. The rest are prococleous. The articular condyle is prominent, with an eccentric apex, located slightly above the centre of the articular surface. The caudal series MPCA 1501, which includes 27 articulated vertebrae, belong to a juvenile. The arch is relatively short and small in relation to the volume of the centrum. It slopes slightly cranially. The prezygapophyses are relatively long, but shorter than in *Aeolosaurus*. The postzygapophyses are attached to the base of neuropophysis, at the anteroposterior midpoint of the vertebral centrum. The neuropophysis is short and almost vertical in the anterior caudal vertebrae.

Girdles and limbs

The scapula has a slightly expanded lamina. The angle between the shaft and the ridge is less than in *Antarctosaurus wichmannianus*. The area of the supraglenoid depression of the proximal expansion of the scapula is smaller than in *Antarctosaurus*. There is a rugosity for muscular attachment on the medial face, close to the upper edge and at the union of the scapular plate with the proximal expansion, which is equivalent to the prominence present in *Saltasaurus loricatus*. The deltoid apophysis is much shorter and less sharp than in *Antarctosaurus wichmannianus*.

The only specimen referred to *T. araukanicus* from the Cinco Saltos locality was a distal end of a humerus. It is slender, characterised by a narrow distal end compared to the humeri of *Saltasaurus* and *Argyrosaurus*.

Huene (1929a) assigned to '*Laplatasaurus*' *araukanicus* a complete humerus (Plate 5, 6) which Lydekker (1893) had previously assigned to '*Titanosaurus*' *australis*. In this work, I refer this specimen to *Titanosaurus* sp. because it comes from a different stratigraphic unit than the lectotype. Moreover, just a humerus in the previously described context does not provide reliable evidence to refer it to this species.

Various radii of juveniles (MLP CS 1167/1173/1174) and a distal half of a left radius (MLP CS 1299) were assigned to *Titanosaurus*? (= *Laplatasaurus*) *araukanicus* by Huene (1929a). The latter is a slender bone, with well defined longitudinal ridges on the ulnar side. There are only five isolated metacarpals with a low robustness index which might belong to *Titanosaurus araukanicus*. Some of these seem to belong to juveniles (MLP CS 1192/1196). Other metacarpals obtained at Cinco Saltos are much longer and slender, and certainly represent adults of this species.

A left pubis (MLP CS 1059) is the only one referred to this species. It is a long and narrow bone which notably contrasts with that of *Argyrosaurus superbus*? and *Saltasaurus loricatus* described below. The lateral margin is less concave than in *Saltasaurus* and the distal end is relatively thin.

A right tibia (MLP CS 1128—Pl. 5:1a, 1b) is part of the lectotype of *Titanosaurus araukanicus*. It is a long, slender bone, less robust at the ends than *Antarctosaurus wichmannianus*, and easily differentiated from the species of *Saltasaurus*, *Neuquensaurus* and *Aeolosaurus* because of its slenderness. The depression situated on the fibular side of the cnemial crest is more extended than in *Antarctosaurus*. The distal condyles are not well defined in the lectotype owing to poor preservation.

The right fibula (MLP CS 1127—Pl. 5:2a, 2b & 2c) is the other element included in the lectotype. It is long, straight, and slender. It shows a strong double lateral tuberosity, with the lower prominence similar to that of *Saltasaurus*, which is oriented obliquely to the shaft of the bone forward and above to behind and below. It is in the centre of the bone. The remaining prominence stands out marking the inferior part of the plate situated in the anterosuperior angle of the proximal area. This tibia greatly resembles, in morphological details and proportions, that assigned to *Titanosaurus indicus* by Swinton (1947).

Comments

As mentioned above, the tibia and fibula of the lectotype of *Titanosaurus araukanicus* are very similar to those referred to *Titanosaurus indicus* by Swinton (1947). This

form is notably similar in its general morphology and proportions, particularly when considering the slenderness of the long bones, the limited development of the distal articulations, and the morphology of the proximal half of the external face of the fibula (Pl. 5:4) with its double lateral tuberosities. On the other hand, some differences of detail allow the South American material to be interpreted as a distinct species. These differences are seen in the caudal vertebrae, whose centra are relatively much longer and laterally compressed in *T. indicus*, and their more flattened lateral walls, which are taller and vertically oriented.

The differences from *Saltasaurus* and related forms are clear and obvious. They are smaller in size, but characterised by the robustness of the limb bones and the widening of the ends of the humerus, ulna, and tibia. There are outstanding differences observed in the caudal vertebrae: *Saltasaurus* and related forms have a developed cancellous structure in the centra, a feature not present in *Titanosaurus araukanicus*. Also, the caudal centra of *Saltasaurus* and *Neuquensaurus* differ in being depressed, and the neurapophysis slopes backwards with short prezygapophyses. The lateral walls are convex in the dorsal-ventral direction. The scapula is different, since it does not possess the process for the muscular insertion on the anterosuperior edge characteristic of *Saltasaurus*, *Neuquensaurus*, and *Aeolosaurus*.

The similarity with *Aeolosaurus rionegrinus* is limited to the general morphology of the caudal vertebrae although, also, in this species the prezygapophyses are very highly developed longitudinally and consequently the facets of the prezygapophyses are located well forward upon the anterior half of the centrum, and the neural spine slopes more forward than in the anterior caudals.

The large and heavy titanosaurids such as *Antarctosaurus* and *Argyrosaurus* have larger and more robust limb bones with greatly expanded articular ends of the tibia and the fibula.

The criteria of Huene (1929a) were used here in relation to the greater part of the specimens assigned to the species. However, most of the elements are represented in the lectotype and very probably do not belong to the same individual, but their size, robustness and general morphology is consistent with those referred to *Titanosaurus indicus* described by Swinton (1947).

I have restricted reference to *Titanosaurus araukanicus* to specimens found in the lower level of the Allen Formation, from Cinco Saltos and Lago Pellegrini localities. Specimens from other localities and different stratigraphic levels (Neuquén-Río Colorado Formation, Bajo La Carpa Member; General Roca-Río Colorado Formation, Anacleto Member; and Rancho de Avila-Neuquén Group *sensu lato*) have been assigned to *Titanosaurus* sp.

Titanosaurus? nanus Lydekker 1893
Nomen dubium Plate 7:2a, 2b, 3a, 3b

Titanosaurus? nanus Lydekker 1893,
p. 8, Pl. 3, Figs 1 and 3; Steel 1970, p. 77;
Olshevsky 1978, p. 28.

Holotype. MLP Ly 18/19. Incomplete cervical and dorsal vertebrae.

Locality. Right bank of Río Neuquén, between 2 and 4 km before the railway bridge which crosses this river, very close to the city of Neuquén.

Stratigraphic Position. Neuquén Group, Río Colorado Formation, Bajo de La Carpa Member?

Age. Late Cretaceous, probably Campanian.

Description

The cervical vertebra MLP Ly 19 (Pl. 7:2a, 2b) is the last of the series. Its preservation is poor and it lacks the pre- and postzygapophyses, part of the neural spine and the diapophysis and parapophysis. The centrum is relatively low and short, and has an enlarged lateral depression.

The dorsal vertebra MLP Ly 18 (Pl. 7:3a, 3b) is also very incomplete, only the centrum and part of the neural arch are preserved. The neural canal is relatively large and the pleurocoel is reduced as it generally is in titanosaurids. It is somewhat larger than in *Saltasaurus* and similar to that of *Neuquensaurus australis* (Pl. 57:3, 4). Note the defined edges of its pleurocoels.

Comments

These specimens are poorly preserved and do not present morphological details which permit clear identification to the generic or specific level. Lydekker (1893) distinguished this form of *Titanosaurus australis* by its small size and proposed the possibility of considering it as a different genus. However, the morphology and proportions as well as its geographic and stratigraphic origin suggest that these specimens may eventually be referred to *Neuquensaurus* sp.

cf. *Titanosaurus* sp.
Plates 8 and 9

Locality. Peirópolis, close to Uberaba, State of Minas Gerais, Brazil.

Stratigraphic Position. Lower and middle levels of the Baurú Formation. Considered by other authors as a facies of the Baurú Formation.

Age. Late Cretaceous, Senonian.

Material. DGM 'Series C'. Final sacral vertebra and 18 articulated caudal vertebrae.

Description

Anterior caudals

The first caudal is biconvex, with the anterior articular surface less convex than the posterior. The centra of the anterior caudals are comparatively much longer than

<i>Titanosaurus</i> sp. 'Series C' of Peirópolis, Brazil							
Caudal Vertebra	1 ^a	2 ^a	3 ^a	4 ^a	5 ^a	6 ^a	8 ^a
Length	10.7	13.2	3.5	13.0	12.0	11.5	12.0
Length without posterior articular condyle	9.0	8.5	9.5	10.0	9.6	9.2	9.2
Total height	29.5	25.5	24.5	22.0	21.0	19.5	28.5
Minimum width of the centrum	—	6.2	5.2	4.7	4.3	3.9	3.5
Height of anterior articular surface	13.2	12.0	11.8	10.0	9.8	8.9	8.5
Width of the anterior articular surface	13.2	13.2	11.6	11.2	10.5	10.0	9.6
Maximum width	28.0	27.5	26.0**	23.0	21.5	19.5	16.0**
Distance between pre- and postzygapophyses	12.0	12.0	11.0	11.0	11.0	11.0	11.0

Table 2a

<i>Titanosaurus</i> sp. 'Series C' of Peirópolis, Brazil										
Caudal Vertebra	9 ^a	10 ^a	11 ^a	12 ^a	13 ^a	14 ^a	15 ^a	16 ^a	17 ^a	18 ^a
Length	11.4	11.4	11.0	11.5	11.0	11.5	11.8	12.0	12.2	12.0
Length without posterior articular condyle	9.2	9.7	9.5	9.0	9.0	9.5	9.5	10.0	10.0	9.5
Total height	28.0	16.5	15.9	15.5	15.3	14.7	14.3	13.3	12.7	11.7
Minimum width of the centrum	4.1	5.2	4.5	3.2	3.1	2.6	2.7	3.0	5.0	5.0
Height of anterior articular surface	—	6.4	7.2	7.4	6.8	7.3	6.6	6.0	6.1	8.1
Width of the anterior articular surface	9.7	8.7	8.0	7.2	6.9	6.7	6.7	7.0	7.0	6.8
Maximum width	11.0	9.0	8.5	7.5	7.0	6.5	6.5	6.0	5.5	5.5
Distance between pre and postzygapophyses	11.0	10.0	10.5	10.0	10.0	10.5	10.5	10.0	12.5	12.0

Table 2b

those of 'Series B'. The lower edge of the lateral face is appreciably shorter in this series. The concavity of the lateral face is less pronounced. The transverse processes of the first caudals are relatively short and simple, clearly different from those of *Saltasaurus loricatus*, which has very long transverse processes. The neural arch is short and slopes somewhat forward. The neural spine inclines slightly backwards, nevertheless it is long, the width is not greater than the length in a proximal section to the apex of the spine, as it occurs in *Saltasaurus loricatus*. The spine is strengthened forward and backwards by the pre-spinal and post-spinal laminae, which are well developed. Their anterior edge forms an obtuse angle with the upper margin of the prezygapophysis. These are not even as large as in *Aeolosaurus* and the 'Series A' from Peirópolis which is discussed further on in this chapter. The facets of the postzygapophyses are laterally oriented and situated above the posterior half of the centrum.

Middle Caudals

These are characterised by having very high and very narrow centra, with rather vertical lateral walls, which are slightly concave and rectangular in form. The transverse processes are reduced to small prominences. The ventral face of the centrum is narrow, especially at half its length.

The neurapophysis is markedly compressed laterally. The caudal vertebrae 13, 14, and 15, are very similar to the type of *Titanosaurus indicus* in their morphology and proportions. The caudal vertebrae of the Indian species differs by having more laterally compressed centra, and the articular facets of the hemapophyses more prominent.

Comments

This caudal series includes 13, 14 and 15, which are very similar to the type of *Titanosaurus indicus*. However, the latter species has a more compressed centrum. This form shares the peculiarity of possessing ventral faces that are relatively narrow and lateral walls longitudinally concave, which occur in other specimens assigned to the genus *Titanosaurus*.

This specimen strongly differs from the caudal vertebrae of *Saltasaurus loricatus* and *Neuquensaurus australis*, which have clearly depressed and wide centra, with a markedly concave ventral facet.

The caudal vertebrae of *Argyrosaurus superbus*? described later, shows strong differences which include more stout centra and a longer neural spine. The articular facets of the postzygapophyses situated more posteriorly than in the 'Series B' (Pl. 15) from Peirópolis that is

described below. In *Aeolosaurus* this condition is even more accentuated.

This material was obtained by Dr LL I Price who was studying it at the time of his death. Unfortunately, it has not been possible to infer possible associations between the vertebral series and limb bones found at Peirópolis. These data could probably be found in the field notes of Dr LL I Price, which could not be studied at that time.

Genus *Aeolosaurus* novo

Type species. *Aeolosaurus rionegrinus* novo

Distribution. Late Campanian–Maastrichtian of the Río Negro Province, Argentina.

Diagnosis. The same as for the type species.

Aeolosaurus rionegrinus novo
Plates 10, 11, and 12

Holotype. MJG-R 1. Seven anterior caudal vertebrae, right and left incomplete scapulae, right and left humeri, right ulna and radius, right and left ischia, five metacarpals, right tibia and fibula, an astragalus, and indeterminate fragments.

Locality. Casa de Piedra, ‘Estancia’ Maquinchao, Río Negro Province.

Stratigraphic position. Angostura Colorada Formation (Volkheimer 1973).

Age. Late Cretaceous, Late Senonian.

Diagnosis. Caudal vertebrae with compressed centra, with high lateral walls and narrow ventral face, from the 3rd–4th caudal. Prezygapophysis longer than in any other known titanosaurid, projecting forward and upward on the anterior caudals, and slightly forward on the 4th caudal. Neural arch inclined somewhat forward. Neurapophysis slightly inclined forward, situated on the anterior half of the centrum. Facets of the postzygapophyses more inclined than in *Saltasaurus*, almost parallelling the sagittal plane in anterior caudals, and located on the anterior half of the centrum. Hemapophysis with separated articular ends. Articular

facets of hemapophysis divided into two angled surfaces. Wide scapular lamina, distally expanded. Prominence for muscular attachment upon the internal face close to the upper margin of the scapula, as in *Saltasaurus loricatus*. Humerus robust with a prominent apex on the deltoid crest for the insertion of the pectoral muscle. Metacarpals relatively short and stout as in *Saltasaurus loricatus*. Pubis with wide distal end of pubic lamina.

Description

Seven anterior caudal vertebrae (Pls 10, 11) of one individual, beginning with the 3rd caudal, were recovered from Casa de Piedra. These elements represent the anterior region of the tail, probably without gaps.

The most anterior vertebra present is probably the 2nd caudal. Of this vertebra, only the centrum and the lateral indication of the bases of the transverse processes are preserved, the plate is inclined forward. This vertebra and the ones immediately behind it, have a wide and somewhat flattened centrum. The 3rd? caudal (Pl. 10:1a–d) has a wide and somewhat depressed centre. The ventral face is broad and short. It has a pleurocoel-like depression on the right side. The base of the neural arch is very short, almost laminar, with the plane inclined forward. The neural spine was not preserved. The prezygapophyses are notably longer and project above and somewhat forward, following the same plane as the neural arch. The 4th? caudal (Pl. 10:2a, 2b, 2c) also has a flattened centrum, but on top of the ventral face a longitudinal depression begins to form, marking the edge which ends at the articular facets of the hemapophyses, only lightly touching the edge of the anterior of the ventral face of this vertebra, but well developed on the posterior edge. The lateral face of the centrum is significantly concave anteroposteriorly. The neural arch is a thick lamina slightly inclined forward. The facets of the prezygapophysis are wide. The 5th? caudal preserves the centrum, transverse processes and the neural arch with the prezygapophysis. The centrum has a narrow ventral face, the lateral wall is concave in the anteroposterior direction. The 6th? caudal (Pl. 10:3) has a somewhat broad anterior face. The lateral walls of the centrum are markedly concave and the ventral face narrow and indented above. The posterior articulation is characterised by its

<i>Aeolosaurus rionegrinus</i> MJG-R 1							
Caudal Vertebra	3 ^d	4 ^a	5 ^a	6 ^a	7 ^a	8 ^a	9 ^a
Total length	17.0	17.0	15.0	16.0	16.0	16.5	14.5
Length without posterior articular condyle	7.5	11.0	11.0	12.0	11.0	11.0	10.5
Total height	—	33.0*	19.0*	—	—	21.5	20.5
Maximum width	20.0*	27.0	22.5*	26.0	14.5*	15.5	14.0*
Minimum width of ventral face of the centra	13.0*	10.0	9.0	7.5	5.0	5.0	6.0
Height of anterior articular surface	13.5	16.0	15.0	14.0*	14.0	13.5	12.0
Width of the anterior articular surface	18.0	14.0	18.5	17.0*	14.5	13.5	12.5
* Measurements taken from incomplete part.							

Table 3

prominence with an eccentric apex located well above the centrum's axis. The neural arch is inclined forward. The prezygapophysis is very large and almost horizontal.

The centrum of the 7th? caudal (Pl. 11:1a–d) is quite similar to those described above. However, a notch under the neural canal affects the outline of the anterior articulation. The anterior end of the centrum is slightly wider than high. The postzygapophyses are against the posterior part of the base of the spine, immediately above the neural canal. The facets of postzygapophyses are almost vertical. These facets are situated above the anterior half of the centrum. The distal end of the neural spine is situated even more forward. The shaft of the prezygapophysis has a triangular section on this vertebra.

The 8th? caudal (Pl. 11:2a–c) retains the basic characters of the anterior vertebral centra. However, the neural arch, prezygapophyses, postzygapophyses and the base of the spine are better preserved than in the rest of the specimens. The prezygapophyses have facets with an almost circular outline. The postzygapophyses are similar to those of the 6th? caudal. The neuropophysis, which is not complete, is strengthened by a medial postspinal lamina. The preserved part of the neural spine inclines slightly forward.

Both scapulae (Pl. 11:4a, 4b) were preserved incomplete. The right one lacks an important part of the supraglenoid expansion. The scapular lamina is broad and relatively short, and somewhat expanded at the extreme distal end.

Close to the upper margin and close to the junction of the lamina with the proximal expansion, there is a process for a muscular attachment similar to that present in *Salitasaurus* and *Neuquensaurus* although less sharp, but much more developed than in *Titanosaurus araukanicus*.

The humeri (Pl. 12:1, 2) are not well preserved. They are robust, broad in the proximal expansion, with the prominence for the insertion of the pectoral muscle well developed on the deltoid crest. They clearly differ from the humeri assigned to *Titanosaurus* by their robustness. The ulna does not show significant differences of diagnostic value. The radius is very well preserved. It is a straight, robust bone similar in part to that of *Salitasaurus loricatus*, although the crests on the cubital side do not have the prominences as in the former genera. The planes which include the maximum width at the ends of the bone, are rotated some 90°.

The pubis is incomplete, preserving only the distal end of the pubic lamina. It is very broad, but thin. Both incomplete ischia (Pl. 12:5a–b, 6a–b) are preserved. The iliac process is short but well defined. The distal projection is short in relation to that seen in Jurassic sauropods such as *Apatosaurus* and *Camarasaurus*, and flat. The contact with the pubis is straight and very long, something like that seen in *Alamosaurus sanjuanensis* (Gilmore 1922) and the bony plate that supports it is rectangular, the minimum distance between the articulation with the pubis and the external edge

Aeolosaurus rionegrinus MJG-R 1				
Humerus	Right	Left	Radius	
Length	92.5	95.5	Length	58.0
Proximal maximum width	30.5*	30.5*	Proximal maximum width	18.0
Distal maximum width	30.5	27.5	Distal maximum width	17.0
Perimeter of minimum section	43.5	42.0	Perimeter of minimum section	26.0
Robustness ratio	1.02	0.92	Robustness ratio	0.45

Table 4

Aeolosaurus rionegrinus MJG-R 1				
Ulna		Tibia		
Length	59.5	Length	67.0	
Proximal articulation width <u>A</u>	25.0*	Proximal maximum width	30.5	
Proximal articulation width <u>B</u>	23.0*	Distal maximum width	22.5	
Proximal articulation width <u>C</u>	22.0	Perimeter of minimum section	0.54	
Distal maximum width	31.0	Perimeter of minimum section	—	
Robustness ratio	—			
* Measurements taken from incomplete part.				

Table 5

resembles that of *Alamosaurus*, but even more those of *Saltasaurus* and *Neuquensaurus*.

The tibia (Pl. 12:7) is very robust at the proximal end, and has a very thick cnemial crest. The depression situated on the posterolateral face of the latter structure is deep and long.

The fibula (Pl. 12:8a, 8b) has a sigmoid outline and is fairly robust, resembling in both aspects the fibula of *Saltasaurus*. The lateral tuberosity is simple, quite similar to that present in the latter genus and *Neuquensaurus*.

The right astragalus (Pl. 10:4a, 4b) is complete. It has an approximately oval outline in proximal view. Its transverse diameter is relatively reduced, very similar to those seen in other known titanosaurid astragali. The ascending process is high. Above this process there is an almost flat rectangular surface which descends anteriorly, forming part of the articular surface with the tibia. On the lateral wall of this process there is a concavity, which corresponds to the articulation with the fibula, while on the medial side there is a deep depression.

<i>Aeolosaurus rionegrinus</i> MJG-R 1					
Metacarpals	14	12	17	11	12
Length	27.0	25.0	31.0	30.0	29.0
Proximal maximum width	13.0	11.0	10.0	11.0	15.0
Distal maximum width	9.5	8.5	9.0	9.0*	10.0
Perimeter of minimum section	17.5	18.5	18.0	16.5	18.0
Robustness ratio	0.64	0.74	0.58	0.55	0.62
* Measurements taken from the preserved half.					

Table 6

Five metacarpals probably belonging to the same manus, are preserved. They are relatively short and robust in comparison with those assigned to *Titanosaurus* from the Allen Formation, and resemble the proportions of those of *Saltasaurus loricatus*.

Comments

Aeolosaurus rionegrinus has a mixture of the peculiar features of very different titanosaurids such as *Saltasaurus* and *Neuquensaurus*, and *Titanosaurus*. The caudal centra of *Titanosaurus* and *Aeolosaurus* are similar in the following features: ventral face of the centrum very narrow; lateral walls of this structure inclined somewhat downward; the neural spine is laterally compressed and facets of the postzygapophyses laterally oriented. However, the prezygapophysis are appreciably longer than in *Titanosaurus*, and the articular facets have a larger diameter. The neural spine and the facets of the postzygapophysis are placed farther forward than in *Titanosaurus*, in relation to the centrum.

Saltasaurus and *Neuquensaurus* resemble *Aeolosaurus* in having stout limb bones. The scapula has a similar prominence for muscular attachment on the medial face, although less developed. The humerus is as robust as in *Saltasaurus* and *Argyrosaurus* and clearly distinct from *Titanosaurus*. *Saltasaurus* and *Neuquensaurus* also share with *Aeolosaurus* the possession of an ischium similar to that of *Alamosaurus sanjuanensis* (Gilmore 1922; Pl. 2:1, 2), which differs only in having a longer and wider ischiaotic lamina, and a shorter pubic peduncle.

Aeolosaurus is a late titanosaurid found in association with Late Senonian South American hadrosaurs.

Aeolosaurus rionegrinus?
Platc 6, 9a-e

Locality. Estancia Los Alamitos, to the south-east of the Cona Niyeu, very close to the northern border of Chubut Province, in the south-east region of Río Negro Province.
Stratigraphic Position. Los Alamitos Formation (Bonaparte et al. 1984).

Age. Late Cretaceous, Campanian-Maastrichtian (Bonaparte et al. 1984).

Material. A series of partially articulated caudal vertebrae consisting of 15 elements temporarily stored in the Musco Argentino de Ciencias Naturales 'Bernardino Rivadavia'.

Description

The series of caudal vertebrae is very similar to *Aeolosaurus rionegrinus*. The centrum of the anterior caudal vertebra is ventrally broad and relatively short, with a concave and short ventral face. The posterior articular facets are strongly convex, having a prominent apex, and which is a little higher than in *Titanosaurus*. The lateral walls are somewhat concave anteroposteriorly. The neural arch is situated on the anterior part of the centrum and is slightly inclined forward. The prezygapophyses have very long shafts, which are oriented forward and upward. The laterally compressed neurapophysis is almost vertical, and is

<i>Aeolosaurus rionegrinus?</i>								
Caudal Vertebra total length	20.0	21.0	20.0	20.0	19.5	19.5	18.0	18.0
Length without posterior articular condyle	10.5*	14.0	14.5	±13.5	14.0	±13.0	12.5	12.5
Total height	—	34.5	32.0	31.5	27.0	30.0	26.5	25.5
Minimum width of the vertebral centrum	13.5*	±9.0	8.0	—	10.5	8.5	7.5	6.7
Height of anterior articular surface	13.5*	—	14.5	—	13.0	13.0	14.0	12.5
Width of the anterior articular surface	21.0	—	—	—	15.5	11.0	12.0	13.0
Maximum width	—	—	—	—	15.5	14.0	17.0	14.5
Distance between pre- and postzygapophyses	—	17.0	±15.5	—	17.0	17.0	16.0	16.5
* Measurements taken from incomplete part.								

Table 7

situated above the anterior half of the centrum. The facets of the postzygapophysis are attached at the base of the neural spine, facing laterally.

The medial caudal vertebrae have centra which become progressively taller posteriorly in the sequence. The neural spines progressively increase their inclination backwards. The last vertebrae recovered of this series is amphicoelous, a feature documented in other titanosaurids.

Comments

These vertebrae have a notable resemblance to those of *Aeolosaurus rionegrinus* in the centrum's morphology, the characteristics of the neural arch, the position and length of the prezygapophysis, and in the orientation and relative position of the postzygapophysial facets.

The result of the comparison of these specimens with other genera is that they conform with those of *Aeolosaurus rionegrinus*.

The most important item in this series is the presence of an amphicoelous vertebra. Although this is little known, it has been described earlier by Huene (1929a) who said that this type of vertebrae had been found at the Rancho de Avila locality (MLP Av 1005/1013) and Cañadon Valeche. He referred them to the genus *Macrurosaurus*.

Genus *Saltasaurus* Bonaparte and Powell 1980

Saltasaurus Bonaparte and Powell 1980

Type species. *Saltasaurus loricatus* Bonaparte and Powell 1980

Distribution. Late Cretaceous (Late Campanian?, Early Maastrichtian) in the Province of Salta, Argentina.

Diagnosis. The same as for the type species.

Saltasaurus loricatus Bonaparte and Powell, 1980
Plates 18–55

Saltasaurus loricatus Bonaparte and Powell 1980, pp. 20–23, pls 3–6; Powell 1980, pp. 41–43, Fig. 1; Powell 1992, 165–230

Holotype. PVL 4017-92. Complete sacrum fused to two ilia.

Locality. El Brete, Department of Candelaria, in the south of Salta Province, Argentina.

Stratigraphic position. Lecho Formation, Balbuena Subgroup, Salta Group.

Age. Late Cretaceous, Senonian, Campanian? - Maastrichtian.

Hypodigm. All the specimens identified as PVL 4017 and also the specimens CNS-V 10.023 and 10.024 corresponding to at least 5 adult and sub-adult individuals, which include 3 distinct cranial fragments, an axis, 14 cervical vertebrae, 20 dorsal vertebrae, 3 sacral vertebrae, 26 caudal vertebrae, 4 scapulas, 3 coracoids, 4 external plates, 10 humeri, 5 ulnae, 4 radii, 5 metacarpals, five ilia, 4 pubes, 2 ischia, 5 femora, 5 tibia, 4 fibulae, 7 metatarsals, 6 dermal plates and 4 associated small dermal ossicles. The numeration and characteristics of the specimens are detailed in the description of each specimen.

Modified diagnosis. Skull with the upper temporal aperture far more reduced than in *Antarctosaurus*, dorsally closed by the coalescence of the parietal and the frontal, complete basisphenoid with a triangular shape in the ventral view, the base is transversally narrow with a pronounced sagittal crest, the *fenestra ovalis* opens for the passage of the IX–XI cranial nerves, the basiptyergoid processes are united at their proximal ends. Cervical vertebrae are relatively shorter and broader than in the known titanosaurs. The centra of the dorsal vertebrae are without 'keels'. Neural spines are distally extremely stout and rounded. Diapophyses with a flat dorsal surface at their distal end. Sacrum with six fused vertebrae, with convex anterior and posterior articulations. The first caudal vertebra is procoelous. The neural spine broad and anteroposteriorly compressed, inclined backwards in the first caudal vertebrae. Scapula with a medial prominence close to the anterodorsal edge. Long bones relatively short and robust. Metacarpals much shorter than in

Antarctosaurus and *Argyrosaurus* and those referred to *Titanosaurus*. Ilium with preacetabular lamina long and strongly curved outward. Intradermic ossicles, and dermal scutes.

Description

The skull of *Saltasaurus loricatus* is generally similar to the one described by Huene (1929a) as *Antarctosaurus wickmannianus*. The two sets of articulated cranial bones herein described belong to adult individuals. Strong ossification at the sutures precludes in most of the cases, determination of the different elements.

Posteroventral view (Pls 19a and 47:2b)

The long paroccipital processes which are curved down and forward, and are amongst the most striking features in occipital view, and resemble in form with these elements in hadrosaurids. This morphology, uncommon in the Saurischia, can be seen as well in *A. wickmannianus*, although these processes are not preserved completely in the material assigned to that species. The occipital condyle is almost perpendicular to the basicranial axis, and its articular facet, of nearly rhomboidal shape, faces downwards. The supraoccipital has a medial tuberosity, which projects both from the plane of the occipital as well as from the cranial roof. On the occipital plane, this tuberosity shows a longitudinal depression coincident with the sagittal plane. The suture between the frontal and orbitosphenoid + laterosphenoid is clearly seen. In the specimen PVL 4017-161 (Pl. 19b) the parietal is absent, but its articular surface with the paroccipital process can be seen. That surface is approximately 1 cm broad and extends over the paroccipital process for about 3 cm. Supraoccipital or exoccipital sutures cannot be seen in any of the material. A line of rugosities or prominences is present which presumably mark the boundary between the two bones for such are found in this suture in other sauropods. The occipital shows a small elongated prominence at each side of the foramen magnum, about 1 cm long, oblique to the medial plane.

Exoccipitals as well as opisthothotics participate laterally in the formation of the paroccipital process. This structure projects first downwards and then outwards, and the distal end, which is progressively narrower, forms a right angle with the proximal region and projects forward.

The foramen for the 12th cranial nerve opens backwards near the ventral edge of the exoccipital, between the base of the paroccipital process and the neck of the occipital condyle. The basioccipital forms almost the whole of the occipital condyle, while the exoccipital seems to be restricted to the superolateral corners and the lateral walls of the condyle. Meanwhile, the exoccipital probably forms most of the floor of the neural canal, corresponding to the condylar zone. The basal tuberosities of the basioccipital are practically flat and show no clear definition between both halves, contrary to what is seen in *Antarctosaurus wickmannianus* and the diplodocids (Berman & McIntosh 1978). The basiptyergoid

apophyses, with the basal tuberosities, form a wide plane facing the ventral side, fusing along most of the preserved zone (Pl. 19a; 47:2b).

Lateral view (Pls 19b and 47:2a)

Orbitosphenoid and laterosphenoid are totally fused. The suture between them can only be seen near the upper edge of these bones, where both articulate with the frontals. These elements are laminar bones about 7 mm thick, forming a 'V' with their pairs on the opposite side. Orbitosphenoids reach their maximum thickness beyond the foramen of the Optic nerve. Apparently the orbitosphenoids overlap the laterosphenoids. The foramen of the Optic nerve (II) opens through the orbitosphenoid, somewhat posterior to the anterior edge of this bone. Its shape is oval and its diameters are 8 x 6 mm. This foramen is separated by 1 cm of bone from its opposite number. Behind and slightly above the foramen of the Optic nerve, there is a small foramen (2 mm wide), corresponding to the Trochlear nerve (IV). Below these foramina is the one for the oculomotor (III) foramen. It is almost circular in outline, and 4 mm in diameter. The position of the openings of these nerves rest in the suture lines of the orbitosphenoid and the laterosphenoid, as can be deduced from observations of other sauropods such as *Diplodocus* (Berman & McIntosh 1978).

The orbitosphenoid complex is limited below by the presphenoid and basisphenoid. The laterosphenoid has on its posterior edge a crest extending over the opening of the Trigeminal nerve (V) known as *crista antotica* (Berman & McIntosh 1978). This wing of the laterosphenoid contributes to the formation of the posterior wall of the orbital cavity which separates it from the supratemporal fossa. Its articulation with the frontals is clearly visible in PVL 4017-162 (Pl. 47:1a). The frontal bone is missing in PVL 4017-161 (Pls 19b and 47:2a), and the sutural plane with the orbitolaterosphenoid complex is visible. It broadens backwards reaching its maximum thickness at the posterodorsal corner, forming the *crista antotica*. The trigeminal (V) foramen is located between the laterosphenoid and the proötic. Its diameters are 8 mm x 6mm. The proötic and the opisthotic are completely fused. The proötic adheres upwards to the anterior face of the proximal segment of the paroccipital process. The latter leads downward in a process that follows the lateral edge of the basiptyergoid apophysis. Behind the foramen from which the Facial nerve (VII) emerges, the proötic shows a laterally concave posterior edge, known as *crista proötic* (Berman & McIntosh 1978). The opisthotic is hidden mainly by the proötic, visible in a lateral view above the paroccipital process as well as the great foramen for the IX–XI nerves. Its diameter are 15 mm x 7 mm. The *Fenestra ovalis* opens into the same duct used for emergence of nerves IX–XI, 1 cm inwards of the external edge which bounds the foramen and above the anterior wall of the duct.

A laminar moiety of the basioccipital forms the posterior limit of the opening of the IX–XI nerves. This lamina merges with the ventral edge of the paroccipital process.

Skull Roof (Pls 20 and 47:1a and 4). The posterodorsal region of the skull has been partially preserved in two specimens that appear to be the frontals of juveniles (PVL 4017-162; Pls 20:1 and 47:1 and PVL 4017-211; Pls 20:2 and 47:4). The frontals are divided in two well defined regions: a lateral or orbital and a medial, which along with the opposite half forms part of the roof of the braincase. The orbital portion is ventrally concave forming the posterodorsal part of the orbit. Presuming the orbit was circular, it would have had a diameter of about 8 cm on the basis of the length of arc of curvature preserved on the frontal.

The orbital part of the frontal is ventrally separated from the medial part by the articular area of this bone with the orbitolaterosphenoidal complex. The medial part covers part of the brain case and the olfactory peduncles.

In a dorsal view, the orbital part is convex with the lateral edge marked by small but well defined tuberosities. Separated by a broad 'valley', the medial part of both frontals define an area which shows three prominences, transversely aligned. The larger one is crossed by the sagittal plane. On the anterolateral corner of the frontal is the articular surface for the prefrontal. It only extends above the orbital part of the frontal in the form of a concave surface which draws a right angle with anterior part of the lateral edge of the medial part of the frontal. The anterior margin of the frontal has been preserved only in PVL 4017-211 (Pl. 47:4).

Braincase floor (Pl. 47, 2c)

The floor of the braincase is formed from back to front by the exoccipitals and the basisphenoids. However, the sutures between these elements cannot be seen. Slightly behind the foramen for the Trigemini nerve there is a small opening through which the Abducent nerve (VI) emerges. The pituitary fossa is very deep. On its floor opens the two foramina of the internal carotid, which appear ventrally in the space determined by the angled laminae of the basiptyergoid process. Approximately, in the middle of the preserved part, a hole pierces the lateral lamina of this process, which might be related as well with the passage of the internal carotid.

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Axis	PVL 4017-1
Length of the centrum	7.0
Total height	11.5
Height of the posterior articulation of the axial centrum	3.5
Width of the posterior articulation of the axial centrum	4.0
Minimum width of the axial centrum	2.0

Table 8

Axial skeleton

The axis (PVL 4017-1; Pls 21:1; 48:3) is a rather small element, short, and endowed with a tall, robust neural spine. The centrum has a somewhat prominent, crescent-shaped odontoid process. Beneath and by the sides, it shows a depression corresponding to the intercentrum which has not been preserved. On its sides, it has two lateral pleurocoels, one of which is located above and the other, below the partially preserved parapophysis. The neural arch is high. The prezygapophyses have not been preserved. The neural spine has a triangular transverse section, with an acute angle pointing forwards. Posteriorly, the spine divides in two robust processes conforming to the postzygapophyses. The articular facets of these are slightly bent out and backwards. The neural spine shows small lateral fossae located in the depression bounded anteriorly by a parabolic edge.

Anterior cervical vertebrae (Pls 21:2; 22; 48:4-5; 49:1 and 5)

Three vertebrae of the anterior region of the neck, practically complete, have been recovered (PVL 4017-3/50/139), belonging to adult individuals and a small centra corresponding to a juvenile.

They are long vertebrae with the characteristic cancellous structure in stout parts such as the centra, prezygapophysis, postzygapophysis and diapophysis. The centrum is opisthocelous with articular surfaces that are more broad than tall. The posterior articular surface has a notch in its upper margin corresponding to the floor of the neural canal. The lateral depressions of the vertebral body are elongated showing reduced but deep pleurocoels. The neural arch is low and long. The prezygapophyses are located over the wide laminae of the diapophyses, and reinforced by a strong spinoprezygapophysial lamina. There is a thin one connecting with the neural arch. The prezygapophysial facets are subcircular and bent about 30° towards the medial plane. The articular surfaces are well separated from one another, fixed to lateral projections of the neural arch, and above the anterior part of the diapophysis. The postzygapophyses are long and project behind the posterior articular face of the centrum. They join together through an inter-postzygapophysial lamina that forms the floor of the large postspinal depression.

The postzygapophysis joins the diapophysis through an oblique lamina. From behind the prezygapophysis, and on both sides of the neural spine, exists a markedly concave surface divided by a thin bone lamina that delimits an upper and lower area. Parapophysis and diapophysis constitute wide processes pointing lateroventrally, which delimits a deep canal that coincides with the lateral depression of the centrum.

Posterior cervical vertebrae (Pls 23, 49:3-4)

Five more or less complete posterior cervical vertebrae have been preserved as well as five fragments (PVL 4017- 5/6/7/8/9/40/190/213/214) among which is a small vertebral body of a juvenile. These vertebrae are

<i>Saltasaurus loricatus</i> Bonaparte and Powell 1980										
Cervical Vertebra	PVL 4017-2	PVL 4017-3	PVL 4017-13	PVL 4017-50	PVL 4017-4	PVL 4017-5	PVL 4017-6	PVL 4017-7	PVL 4017-8	PVL 4017-9
Total length	15.5	16.0	16.0	10.0	16.0	16.0	17.5	15.0	—	13.0
Total height	11.0	11.0	11.5	—	14.5	16.0	15.5	17.0	18.0	17.5
Height of posterior articular surface	5.5	5.5	5.5	3.0	10.0	11.0	11.0	11.0	13.0	11.0
Width of posterior articular surface	6.5	7.5	8.0	4.5	7.5	7.5	—	7.0	9.0	8.0
Distance between prezygapophysial facets	5.0	5.0	5.5	—	10.0	13.0	—	18.0	—	14.0
Distance between postzygapophysial facets	4.5	4.5	5.0	—	11.0	—	11.5	13.0	16.0	12.5
Distance between pre- and postzygapophyses	15.0	15.5	15.0	—	12.5	—	—	11.5	—	11.5

Table 9

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Dorsal Vertebra	PVL 4017-11	PVL 4017-13	PVL 4017-14	PVL 4017-15	PVL 4017-16	PVL 4017-135	PVL 4017-136	PVL 4017-137	
Length	15.0	13.5	14.5	14.5	16.0	15.0	16.0	15.0	
Total height	27.0	29.5	26.5	30.0	30.0	33.0	30.0	31.0	
Width of posterior articular surface	—	14.0	9.5	11.0	11.0	13.0	11.0	11.5	
Distance between facets of postzygapophyses.	10.0	12.0	12.0	13.0	11.0	12.0	—	13.0	

Table 10

proportionally shorter and wider than the anterior cervicals. The centrum shows marked lateral depressions, containing reduced, deep pleurocoels sometimes divided by an oblique osseous bar. The posterior articular surface is deep and concave, and has an oval contour with its largest diameter in the horizontal position. A notch on the upper part determines the passage for the neural canal.

The ventral face of the centrum is concave. The prezygapophyses project laterally to both sides of the neural spine, located in this way behind those of the anterior cervical vertebrae. The articular surface of the prezygapophysis is subcircular and bent towards the medial plane and backwards. Behind this, there exists a deep depression that allows the free movement of the prezygapophyses of the previous vertebra. The postzygapophyses constitute stouter and shorter processes than those of the anterior cervicals. As well, in the posterior cervical vertebrae, the arms of the postzygapophyses open in considerably larger angles than in the anterior cervicals. In all the cervicals, the postzygapophysial arms are joined near their base by a bony lamina, more or less horizontal. The neural spine is low and undivided, and connected to the postzygapophysis by a thick spino-zygapophysial lamina. Laterally, it shows two prominent tuberosities. The parapophysis and diapophysis are stout lateral projections pointing slightly downwards, the latter being longer and

narrower than the former, which sometimes fused to the cervical rib. Both structures are laminar, broad and fixed alongside the vertebral body. The reinforcement laminae (diapo-postzygapophysial and spino-prezygapophysial) are thicker than on the anterior cervical vertebrae. The posterior edge of the parapophysis divides towards the base into two laminae. One, diapo-postzygapophysial and the other, linked to the centrum, which delimits a triangular depression.

Dorsal vertebrae

The dorsal vertebrae are short and rather tall. The centrum has a reduced pleurocoel. Cancellous tissue forms all the 'massive' parts of the vertebra. The hollow space is 60% of the total volume of every dorsal element (Pl. 30). This accounts for the lightness of the vertebrae.

Only three incomplete anterior dorsal vertebrae have been recovered (PVL 4017-10/11/12) together with a neural arch of a first dorsal vertebra (PVL 4017-44), PVL 4017-10 (Pls 24:1 and 50:1). It shows a high neural arch, broad but short, attached to the posterior part of the centrum. The prezygapophyses are short and held by two bony pillars supported on a part of the infradiapophysial lamina. The articular facets are subcircular, with a diameter of 6 cm. The diapophyses project laterally from behind the prezygapophyses, perpendicular to the centrum. They are supported by a well developed

infradiapophysial lamina, that forks downwards delimiting between both branches a deep triangular depression. The parapophysis is situated above the anterior branch, low and close to the centrum.

PVL 4017-12 (Pl. 24:2) probably corresponds to the 2nd or 3rd dorsal vertebra. It is incomplete because a large part of the centrum and postzygapophyses are missing. The neural spine is very wide and low. It joins the diapophysis through a strong diapophysial lamina in a subvertical plane. The anterior horizontal lamina is comparatively well developed in relation to the posterior dorsal vertebrae, delimiting an extended infradiapophysial depression. In this element, there is evidence of a postspinal lamina and although not preserved, a broken surface indicates the presence of a prespinal lamina. The postzygapophysial articular facet is very wide, a common occurrence in anterior dorsal vertebrae. The neural arch (PVL 4017-44) is very well preserved, retaining a broad neuropophysis. The prezygapophyses are held on one prezygapophysial column, with more reduced articular surfaces than in the previously described dorsal vertebrae. Diapophyses are short and stout at the end, where a flat dorsal surface can be seen. The parapophyses have articular facets with an 'eye' outline, with the sharp end upwards. They are at the same level of the prezygapophysis, but quite beneath and somewhat in the front of the diapophysis. The neural spine is undivided and has both pre- and postspinal laminae.

The posterior dorsal vertebrae (Pls 26–30; 50:2–3; 51) include the following elements: PVL 4017-13/ 14/ 15/ 16/ 41*/ 42/ 43*/ 47/ 48/ 53*/ 58*/ 59/ 86*/ 135/ 136/ 137/ 138/ 185/ 215. Two sets of articulated vertebrae, with three elements each, have been recovered. PVL 4017-137 (Pls 27 and 51:1) is probably the 8th in one of the above mentioned sets. The centrum has expanded ends and a reduced pleurocoel. The neural arch is high, narrow, slightly wider on the anterior part under the parapophyses. The prezygapophyses have not been preserved. The postzygapophyses are attached to the neural spine through suprapostzygapophysial lamina, enlarged on the posterior edge. It joins the diapophysis as well, by another bony lamina: the posterior horizontal. The articular facets of the postzygapophyses bend outwards and backwards. The diapophyses are short and project laterally and upwards, reaching almost the height of the dorsal tip of the neural spine. The diapophysis is linked with the prezygapophysis by a weakly developed anterior horizontal lamina, to the postzygapophysis by a posterior horizontal lamina, and strongly linked to the neural spine by a large supradiapophysial lamina. The neural spine inclines slightly backwards, and is robust at the end. It is reinforced at the base by a strong bony lamina that links it to the diapophysis, the postzygapophysis and the pre- and postspinal lamina. This centrum has three clearly defined lateral depressions: two of them are located under the horizontal laminae, called anterior and posterior infradiapophysial

depressions. The third one is placed lateral to the spine, limited in front by the supradiapophysial lamina and behind by the suprapostzygapophysial lamina and ventrally by the posterior horizontal lamina.

PVL 4017-135 (Pl. 51:2) is the third of the articulated series considered and probably correspond to the 9th or 10th dorsal vertebra. Its general features are similar to the previously described PVL 4017-137. However, it differs by possessing a short and stout centrum, by the more vertical orientation of the spine and a backwards displacement of the parapophysis which is located partially beneath the diapophysis. This alters other characters such as the obliteration of the anterior infradiapophysial depression, showing besides a notable development of two thick infrapapophysial laminae which frame a small triangular depression. The inferior infradiapophysial lamina incorporates, in its ventral part, the infrapapophysial lamina.

The posterior dorsal vertebrae have almost horizontal flat surfaces on the upper parts of the ends of the diapophyses, which can be seen in other vertebrae of the series. There are three vertebrae in a second group of articulated dorsal vertebrae (PVL 4017-42; Pl. 50:3). These are practically complete and probably correspond to the 5th, 6th and 7th dorsal vertebrae. They belong to a young adult. The vertebral body is relatively long, comparable with PVL 4017-137 of the other articulated series. The neural spine bends approximately 45° in relation to the axis of the centrum, being broader in the first of the series, and turning slender backwards.

PVL 4017-138 belongs to a large adult and probably corresponds to a 6th dorsal vertebrae, judging by the similarity of characters which it possesses in relation to the probable 6th dorsal vertebra in PVL 4017-42 series.

Sacrum

Of the three known sacra, the holotype (PVL 4017-92, Pls 31, 55:7) and PVL 4017-93 (Pl. 55:6) are fused to both ilia. The third (PVL 4017-18, Pl. 55:8) is an incomplete sacrum. The holotype includes six fused centra. The anterior articular surface of the first sacral is convex, and the posterior articular surface is convex as well in the last sacral. The first sacral is a recently incorporated dorsal vertebra. Its body broadens at both ends, while the neural arch is similar to that of the posterior dorsals, this one having a lateral depression. The base of the parapophysis is placed high on the neural arch. The neural spine, parapophysis and diapophysis have not been preserved. The centrum of the second sacral has a hardly visible posterior limit. Parapophysis and diapophysis are on the same vertical plane, and are largely laminar. The rib fused to these processes is placed as a vertical lamina, with a subcircular fenestra on its proximal part.

From the 3rd to the 5th sacral vertebrae, the centra are narrow and the limits between them are obscure. Pre- and postzygapophysis are fused to the adjacent vertebrae.

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Cervical Vertebra	PVL 4017-19	PVL 4017-20	PVL 4017-21	PVL 4017-22	PVL 4017-23	PVL 4017-24	PVL 4017-25	PVL 4017-27	PVL 4017-28	PVL 4017-29
Total length	14.0	14.0	13.0	14.5	14.5	13.5	15.5	15.0	15.5	15.0
Length without posterior articular condyle	—	—	—	10.0	8.0	9.0	10.0	11.0	11.0	11.5
Total height	26.0	32.5	—	28.5	28.5	31.0	28.5	—	21.5	—
Minimum width	48.0	51.0	—	26.0	31.5	30.0	24.0	19.0	17.0	—
Height of anterior articular surface	9.0	11.0	7.0	11.0	13.0	14.0	10.5	9.0	9.0	9.0
Width anterior articular surface	12.5	13.0	12.5	16.0	15.5	15.0	11.0	13.0	12.0	11.5
Distance between prezygapophysial facets	—	—	—	6.0	8.0	7.5	8.0	8.0	5.0	—
Distance between postzygapophysial facets	—	—	—	8.0	7.0	7.0	7.5	—	—	—

Table 11

Although the neural spines are not preserved in their entirety, their bases can be seen to be joined by the prespinal and postspinal laminae of successive vertebrae. Diapophysis and parapophysis are fused to the ribs, projecting laterally as laminae with two attachments: the upper contains the diapophysial process while the lower one corresponds to the parapophysis. The rib of the 3rd vertebra shows a small subcircular fenestra on its proximal part. Another fenestra, larger in diameter and adjacent to the ilium, can be seen in the ribs of both the 4th and the 5th sacral vertebrae. All the sacral ribs show a distal broadening, one dorsal and the other ventral, through which they are fused to one another and to the ilium. The distal ventral broadenings of the ribs of the last 4 sacral vertebrae participate together with the ilium in the formation of the articular surface of the acetabulum and in a similar way, to that described in other titanosaurids in this same paper, and in *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka (1977) of the Late Cretaceous of Mongolia.

Caudal vertebrae

The caudal vertebrae of *Saltasaurus loricatus* have depressed, procoelous centra, similar to those of *Neuquensaurus*. Like the cervical and dorsal vertebrae, they have cancellous tissue in the anteromedial region and at least part of the posterior region of the centrum.

First and second caudal (Pls 52 and 53)

The centrum is procoelous, short and rather low and broad. The anterior articular facet is slightly concave and oval in outline. The neural arch slopes about 35° backwards. The neurapophysis is short and laterally expanded, and has a prespinal and postspinal lamina. The articular facets of the postzygapophyses are oval, and oriented in a way in which the longer diameter converges to the sagittal plane.

The transverse process is strikingly long resembling that of the last sacral element. It forms a curved plane in its distal end. The lower edge projects forward beyond the upper one. On the anterior face of the transverse process, exists a proximally located deep depression. On two of the elements (PVL 4017-19/21) there is an elongated

tuberosity for a muscular or ligamentous attachment on the transverse process.

Anterior caudal vertebrae (3rd?-6th?; Pl. 33)

This region is represented by four complete elements (PVL 4017-22/24/25/26). The centra are short and broad. The articular surfaces are more convex than the most anterior caudal vertebrae. The ventral face is broad and slightly concave. The prezygapophyses are stout and short compared to those of *Aeolosaurus* and *Titanosaurus* from Brazil, which have large articular facets. In the case of PVL 4017-23 (Pls 33 and 52:2) part of the surface of an articular structure resembling an hypantrum has been preserved. The postzygapophyses are suspended from the neural spine by thick laminae whose external faces show rugosities for muscular or ligamentous insertion. Their articular facets are large. The neural spine is broad and slightly inclined backwards, with the anterior face divided by a prespinal lamina. From posterior view, the lamina supporting the postzygapophysis delimits a deep depression. The transverse processes are reduced and project downwards and backwards.

Medial caudal vertebrae (Pls 34 and 52:3)

The vertebral centra are longer than those of the anterior caudal vertebrae. The anterior and posterior articular facets are dorsoventrally depressed. The ventral face shows a much narrower longitudinal depression which in *Neuquensaurus* has a medial crest. The neural arch is long and located on the anterior part of the body of the centrum. The prezygapophyses are short processes extended forward with reduced articular facets, somewhat sloped inwards. The neural spine progressively slopes towards the posterior end of the tail. On its anterior face there are two lateral crests that project forward over the wings of the prezygapophysis. The transverse processes are reduced and inclined downwards and backwards.

Posterior caudal vertebrae (Pls 35; 53:6 and 7)

The elements of this region are available in PVL 4017-32/ 38/ 39/ 140/ 141/ 191/ 207/ 218/ 219/ 220. The centra are long and dorsoventrally depressed, expanded at the ends. These caudal elements are low, owing to the reduction of

<i>Saltasaurus loricatus</i> Bonaparte and Powell 1980				
Scapula	PVL 4017-104	PVL 4017-105	PVL 4017-107	PVL 4017-106
Length	37.0	37.0	60.5	64.0
Maximum proximal width	19.5	17.0	—	34.0
Maximum distal width	13.5	13.0	18.0	23.0
Minimum width of the lamina	8.5	—	13.0	15.0

Table 12

the neural spines which persist, starting at the 16th caudal vertebra, to show just a crest on the 20th caudal vertebra. The neural arch is low, and its length corresponds approximately to half that of the centrum and is located on the anterior part of the vertebral centrum. The prezygapophyses are long cylindrical processes that project forward and lack defined articular surfaces. The postzygapophyses are fused, bearing on them the neural spine.

Scapula (Pls 37 and 54:2)

Two scapulas (right and left) of a juvenile (PVL 4017-104/105) and two right scapulas of adults were recovered. The scapula is similar to that of *Neuquensaurus australis* (Huenc 1929a), but relatively broader, showing a wider angle between the axis of the scapular lamina and the crest that frames the supraglenoid depression. The edges of the lamina are sharp except the proximal part of the upper edge, where there is a broadening related to a medially projecting prominence for a muscular attachment similar to that present in *Neuquensaurus australis* (Huene 1929a). The dorsal edge in the narrower region of the lamina is less concave than that of *N. australis*. The posteroventral edge is not as straight as illustrated by Huene (1929a; Pl. 9:3a), but has

a concave outline all along the lamina, a character determined by the distal broadening of the scapular lamina. The thicker part of the scapular blade is in the region of greatest narrowing. In this place the external face is strongly convex. Contact with the coracoid is not well defined. None has ever been found articulated to the scapula. The scapular part of the glenoid surface faces anteriorly and medially.

Coracoid (Pls 38 and 54:1)

Two coracoids, one left (PVL 4017-100/101) and one right (PVL 4017-103) have been preserved. The coracoid has a grossly quadrangular outline, and is endowed with a humeral articular surface. The anteromedial edge is straight and perpendicular to the medial edge. Over the glenoid articulation there is a thickening of the bone which continues as a longitudinal elevation parallel to the anteromedial edge.

The coracoid foramen is placed on the outer face and located with a depression oriented towards the anteromedial edge.

Sternal plates (Pls 39 and 54:6)

These are large laminar bones, quite similar to those

<i>Saltasaurus loricatus</i> Bonaparte and Powell 1980			
Coracoids	PVL 4017-100	PVL 4017-101	PVL 4017-102
Preserved length (perpendicular to the medial edge)	25.0	27.0	28.0
Maximum medial width	24.5	23.0	27.0
Maximum width at the articular facet	11.5	11.0	10.5

Table 13

<i>Saltasaurus loricatus</i> Bonaparte and Powell 1980				
Sternal Plates	PVL 4017-108	PVL 4017-109	PVL 4017-110	PVL 4017-111
Maximum preserved length	61.0	60.0	—	—
Preserved length of the lateral edge	54.0	55.0	38.0	25.0
Maximum preserved width	26.0	27.0	20.0	—
Thickness of the anterior end	6.0	—	6.0	5.5

Table 14

<i>Saltasaurus loricatus</i> Bonaparte and Powell 1980										
Humerus	PVL 4017-70	PVL 4017-71	PVL 4017-69	CNS-V 10023	PVL 4017-62	PVL 4017-63	PVL 4017-64	PVL 4017-65	PVL 4017-66	PVL 4017-67
Length	35.0	37.0	49.0	50.0	54.0	53.0	52.5	52.0	58.0	59.0
Maximum proximal width	19.5	—	25.0	25.5	30.0	30.0	26.0	26.5	28.0	30.0
Maximum distal width	14.0	14.0	15.0	15.0	15.5	—	21.0	22.5	21.0	21.5
Minimum section's perimeter	21.5	21.5	27.0	25.0	31.5	35.0	28.0	35.0	29.5	28.5
Robustness ratio	0.61	0.58	0.55	0.50	0.58	0.66	0.53	0.67	0.50	0.48

Table 15

<i>Saltasaurus loricatus</i> Bonaparte and Powell 1980				
Ulna	PVL 4017-72	PVL 4017-73	PVL 4017-74	PVL 4017-75
Length	43.0	39.0	38.0	40.0
Proximal articulation width a	24.0	—	19.5	—
Proximal articulation width b	20.0	17.5	16.5	17.5
Proximal articulation width c	17.5	—	14.5	16.0
Maximum distal width	—	9.5	10.5	—
Perimeter of the minimum section	26.0	24.0	22.0	22.5
Robustness ratio	0.60	—	0.57	0.56

Table 16

referred to *Neuquensaurus australis* (Huene 1929a: Pl. 9). Two partially articulated sternal plates have been preserved in which the lateral and medial edges can be seen. Based on their structure, it is inferred that the anterior thicker end articulates with the coracoid. The lateral edge, thick and rounded, has a strong externally concave profile. The whole region proximal to this edge is rather thick, while towards the medial side the width is consistently reduced. The anterior end is thickened by means of an obtuse ridge, which extends over the ventral side, starting at the anterior end of the bone, backwards for 8 cm.

The dorsal face of the plate is rather flat and shows no striking details.

Humerus (Pls 40, 48:1 and 54:3)

The humerus is robust and relatively short, the proximal third being very wide and flattened. The distal end is twisted some 35° in relation to the proximal. The proximal edge is sigmoid, with the convexity located on the articular head, and the inner tuberosity and the concavity on the basal zone of the lateral apophysis. In the corner of the lateral apophysis, the proximal edge rises again.

The lateral apophysis is thin, broadening towards the lateral edge, where it forms the deltopectoral ridge anteriorly. The latter is rather short with rounded edges, obliquely arranged in relation to the bone's axis. The anterior depression of the proximal end is very wide. This

depression shows a longitudinal elevation transversally oriented in relation to the long axis of the humerus that is the point of insertion for the coracobrachial musculature. In the posterior or dorsal face of the bone, there are some outstanding rugosities which are sites of muscular insertions. One of the most prominent of these is located on the lateral edge, opposite to the deltopectoral crest. On the anterior face, the distal articular surfaces are clearly distinguishable; of these, the internal is more developed in the anteroposterior dimension. And the lateral one, in the transverse. The radial condyle is well developed. The posterior face of the distal end is broad, showing a broad and deep depression bounded by two supracondylar crests, of which the inner one is the most developed, thin and sharp.

The entepicondyle and ectepicondyle are poorly developed. Upon the medial edge, there is the projection of a slightly developed supra-ectepicondylar crest. Among the available humeri there is a high degree of intraspecific variation. For example the pair PVL 4017-69 and CNS-V 10.023, differ from the other available humeri by the possession of a more rugous and strong insertion area, and by the lack of a concave surface, medial in relation to the previously mentioned area of muscular attachment. The posterior depression bounded by two supracondylar crests is narrower and deeper.

Ulna (Pls 41; 54:4)

Five specimens were recovered (PVL 4017-72-75 and

Saltasaurus loricatus Bonaparte and Powell 1980

Radius	PVL 4017-151	PVL 4017-76	PVL 4017-77	PVL 4017-78
Length (preserved)	26.5	35.0	33.5	23.0
Length (estimated)	28.0	35.0	34.5	23.0
Maximum proximal width	13.0	12.0	11.0	8.0
Maximum distal width	9.5	11.0	5.0	3.5
Perimeter of the minimum section	20.0	15.0	14.0	10.5
Robustness ratio	0.71	0.42	0.41	0.26

Table 17

PVL 4017-151) of two different sizes corresponding to large and medium adults. It is a stout, straight, three-faced element at its proximal end. The medial face of the bone is the broader one. On the proximal half of the bone this face is concave. On the junction with the rest of the faces, it forms acute angles. The anterolateral face is concave in the proximal region, losing this character at the distal end. On the distal half it has an insertion crest for the *pronator teres*. The distal articulation forms a rounded surface with a slight notch on the inner face.

Radius (Pl. 42)

There are two right radii of large individuals (PVL 4017-76-151), the left radius of a young adult PVL 4017-77, and the left radius of a juvenile (PVL 4017-78). The anterolateral face of the radius is rather flat and slightly concave at the proximal end. The ulnar face is strongly convex with a central longitudinal depression bounded by smooth crests, crossing the bone obliquely from anterodorsal to the posteroventral corners. In the smaller of the available radii, the sigmoid shape is more obvious than in the rest of the specimens.

Metacarpals

They are proportionally short and stout in comparison with those of *Antarctosaurus wichmannianus* and *Titanosaurus araukanicus* Huene (1929a). The metacarpal III (PVL 4017-125) has a flat proximal articular surface of triangular outline, while the distal end is slightly convex. The metacarpal IV? (PVL 4017-128) is smaller than metacarpal III. Its proximal articular face is crudely rectangular with a marked lateral projection on one of the anterior corners. The distal articulation is also convex but less broad than metacarpal III. The following

Saltasaurus loricatus Bonaparte and Powell 1980

Metacarpals	PVL 4017-125	PVL 4017-128
Length	14.0	15.0
Maximum proximal width	7.0	7.5
Maximum distal width	7.0	6.0
Perimeter of minimum section	12.0	10.0
Robustness ratio	0.85	0.66

Table 18

specimens, although certainly metacarpals, are of unknown position: PVL 4017-180/126/127.

Pelvic girdle

Ilium (Pls 31 and 55:6-7)

The ilium is low with a long, anteriorly and externally directed preacetabular lamina as occurs in other titanosaurids. The postacetabular process is short and poorly preserved in all the available specimens. The pubic peduncle is broad, transversely expanded, and its anteroposterior thickness is much reduced. The ischiatic peduncle is barely perceptible. The acetabular articular surface is formed mostly by the ilium and the ventral distal expansions of the 3rd to 5th sacral ribs. The outline of the iliac part of the acetabulum forms a parabola with the inflection point located in the joint of the peduncle with the ventral edge of iliac lamina. Elements PVL 4017-93 (left and right ilia fused to the sacrum) and PVL 4017-94 (left ilium fused to the distal end of the last sacral vertebrae) have a small expansion on the anterior end of the iliac lamina. Such an expansion is absent from the holotype. PVL 4017-92 (left and right ilia fused to the sacrum). On it, the preacetabular part of the lamina is slightly broader at the anterior end.

Pubis (Pls 43:1 and 55:9)

PVL 4017-95 is a right pubis. PVL 4017-96 is an incomplete right pubis with its distal half missing and PVL 4017-97/98 consists of two incomplete pubes (right and left) lacking the proximal regions. The pubis is laminar and relatively thin.

Femur (Pls 44, 45:1)

The femora are represented by PVL 4017-79/ 80/ 82/ 83 and CNS-V 10.024. They are long, rather straight and somewhat flattened anteroposteriorly, mainly on their proximal half. A comparatively thin lateral projection of the greater trochanter is present on the proximal half of the femur, with its maximum expansion located one quarter of the distance from the proximal to the distal end of the bone. The greater trochanter forms a dorsoventrally directed ridge on the proximal one-third of posterior face of the femur. The anterior face of some femora have a long rugosity located above the centre of the bone. The femur of *Saltasaurus loricatus* lacks an articular surface which is common in the Jurassic sauropods and

titanosaurids such as *Argyrosaurus*. On the distal end, the medial condyle is the most developed. The depression formed between the two distal condyles is shallow.

Tibia (Pls 45 and 55:2,4,5)

The tibia PVL 4017-84 (Pls 45:1 and 55:4) is characterised by the possession of markedly stout ends. The other specimens (PVL 4017-46/65/88- Pl. 55:2) are more slender including PVL 4017-87 which is a juvenile (Pls 45:2 and 55:5).

The proximal end of the tibia has a rather flat articular surface in the middle. The cnemial crest is slightly curved outwards as a thick triangular lamina.

Fibula (Pls 46 and 55:3)

The fibula of *Saltasaurus loricatus* is long, with a sigmoid shape in lateral view. Its external face is convex over all of its extent and is a particularly noticeable feature of the distal half of the bone. A well developed tuberosity extends obliquely from the anterodorsal to the posterodistal region of the bone. The rugosity present on this tuberosity marks the area of insertion for the iliofibular muscle, interpreted by Huene (1929a) as corresponding to the peroneus muscle. This insertion differs notably with that in *Titanosaurus araucanicus* Huene and *Titanosaurus indicus* Lydekker (in Swinton 1947), resembling instead that present in *Neuquensaurus australis*.

The inner face of the diaphysis is rather flattened, turning markedly concave at the distal end. On the basis of the available specimens, the length of the fibula is 59.8% of that of the femur.

Metatarsals

The metatarsals are extremely short and stout. Metatarsal I (PVL 4017-131/122) is very short. Its articular proximal face is crudely triangular with its base dorsal and the apex ventral. On its lateral face there is a facet for its articulation with metatarsal II. Metatarsal V (PVL 4017-121) is flattened and stouter than the one illustrated for *Neuquensaurus australis*. Metatarsal II? (PVL 4017-124) resembles the I in that its proximal articular surface is rather oval. The following specimens, although certainly metatarsals, are of unknown position: PVL 4017-123/133/182.

Dermal armour

One of the most striking features documented in *Saltasaurus loricatus* is the possession of dermal armour, the first recognised among sauropods (Bonaparte & Powell 1980; Powell 1980). It consists of bony plates with a maximum diameter of approximately 12 cm that probably held spikes. Although there is no direct evidence, it is possible that these were arranged in one or two rows along the back and the anterior part of the tail (Pl. 18). Other possible arrangements cannot be discounted at this time. In addition, they had small intradermal bones such as those present in the mylodontid ground sloths, that protected the dorsal part of the body.

Scutes (Pls 76:1, 2, 3)

Six plates have been recovered (PVL 4017-112-116/134). They have a more or less oval outline with irregular margins. The dorsal face is crudely conical and ornamented with numerous irregular rugosities formed by fossae of various sizes. A 'ring' of small tuberosities is located near the margin of the scute. The internal face is almost smooth with irregular grooves arranged near the edge, and approximately perpendicular to it. In some scutes, this face is traversed by a longitudinal crest oriented along the larger diameter. In others, this crest is absent and the ventral face is concave. In scute PVL 4017-115 (Pl. 76:2) small subspherical ossicles are fused to the margin.

Dermal ossicles (Pl. 54:5)

Four groups of associated ossicles preserved in their original position have been recovered (PVL 4017-117/118/119/120). In addition, there are numerous other ossicles which are isolated or in groups. These bony elements are subspherical and irregular in form. Their average diameter is around 7 mm.

They are arranged in contact forming an irregular mosaic with a density of 27 elements per 10 cm². Only in the case of the group of ossicles PVL 4017-119, is there a visibly larger element among the rest.

Comments

Neuquensaurus (= *Titanosaurus* sensu Huene 1929a) is the genus with closest affinities to *Saltasaurus*. Both taxa are represented by medium to small sized forms (within the sauropod context), showing a striking resemblance to one another in the morphology and proportions of the limb bones. In addition, they share depressed caudal centra with cancellous structures in at least part of the sequence, although differing in degree of development. Even so, there are a number of differences which clearly justify the recognition of two different genera for these forms. The preacetabular projections of the iliac laminae are longer and more expanded in *Saltasaurus*. The postacetabular processes are absent, and a defined ischiatic peduncle such as the one recognised by Huene (1929a) in *Neuquensaurus robustus* (Huene 1929a; Pl. 19:1) is present. The caudals are similar in both genera, except for the first caudal, which is biconvex in *Neuquensaurus* and procoelous in *Saltasaurus*. The ventral depression is very broad in *Neuquensaurus* and usually shows no trace of the sagittal lamina seen in *Saltasaurus*. The cancellous condition is present in all caudal centra, while in *Neuquensaurus* it is restricted to the anterior region. The scapula of *Saltasaurus loricatus* is broader, and the lamina fuses to the proximal part, making a larger angle with the crest that bounds the supraglenoid depression.

Antarctosaurus wichmannianus shows clear differences from *Saltasaurus loricatus* not only in size and general proportions, but in morphological features, braincase, and postcranial skeleton as well.

Antarctosaurus wichmannianus shares with *Saltasaurus* the long and recurved paroccipital processes. Titanosaurids are the only saurichians possessing this derived structure. The main differences are restricted to the morphology of the basal tuberosity of the basioccipital, the basipterygoid process, the supratemporal fossae and the basipresphenoid complex. The scapular lamina of *Antarctosaurus* is narrower and the proximal expansion is broader than in *Saltasaurus*. The metacarpals are longer and the femur has a medial articular facet on the femoral head, absent in *Saltasaurus*.

Titanosaurus araukanicus is more slender. The morphology of the lateral tuberosity of the fibula shows an additional prominence, oriented posteriorly, while the scapula lacks the medial process close to the upper margin. The metacarpals are strikingly longer and more slender than in the titanosaurid of El Brete.

This species shows a set of derived characters in the braincase as well as in the axial skeleton which indicate it is an advanced titanosaurid. This fact is consistent with its late appearance in the Late Senonian of South America. The observed differences in some of the El Brete elements are provisionally interpreted as owing to individual or sexual variation.

Genus *Neuquensaurus* Powell 1992

Titanosaurus Lydekker 1893, p. 4; Huene 1929a, p. 94.

Type species. *Titanosaurus australis* Lydekker 1893.

Distribution. Late Cretaceous, Campanian? –Early Maastrichtian, of Neuquén and Río Negro, Argentina.

Diagnosis. The same as for the type species.

Neuquensaurus australis (Lydekker 1893)

Plates 56, 57, 58, 59

Titanosaurus australis Lydekker 1893, p. 4, Pl. 1,

Fig. 1–6; Huene 1929a, pp. 23–48, pls 2–5 and 7–17; Steel 1970, p. 77; Bonaparte 1978, p. 555, Pl. 264; Bonaparte and Gasparini, 1979, pp. 396–97.

Holotype. MLP Ly 1/2/3/4/5/6. Caudal vertebra (Pl. 58:6).

Locality. Right bank of the Río Neuquén, 2–4 km upstream from the iron bridge which crosses this river, very close to the city of Neuquén, Neuquén Province, Cinco Saltos and Lake Pellegrini, Río Negro Province.

Stratigraphic position. Neuquén Group. Río Colorado, Bajo de La Carpa Member? (Holotype) and Lower Member of the Allen Formation.

Age. Late Cretaceous. Senonian, Campanian? Early Maastrichtian.

Material referred to the species

Vertebrae:

Series Ly 1: MLP Ly D. 711A, 46, 19 (cervical vertebrae); MLP Ly 23, D8, 10 (dorsal vertebrae); MLP Ly 7 (sacral vertebrae) MLP Ly 1, 8, 9, 2, 68, 48, 5, 74, 61, 56, 55, 58, 82, 59, 62, 79, 9, 83 (caudal vertebrae)

Series Ly 2: MLP Ly 42, 90, 70, 64, 4, 112, 76, 53, 57, 73, 85, 39, 45, 60, 71, 6, 80, 50, 49, 77 (caudal vertebrae).

Series Ly 3: MLP Ly 8D, 40, 75, 51, 8D (three vertebrae), 98, 24, 8D (two caudal vertebrae).

Series of Cinco Saltos 1: MLP CS 1311 (atlas-axis), 1147, 1360, 1367, 1361, 1359, 1366, 1362, 1372 (cervical vertebrae); MLP CS 1357, 1373, 1370, 1381, 1361, 1385, 1388, 1386, 1387 (dorsal vertebrae); MLP CS 1390, 1391, 1394, 1404, 1412, 1416, 1418, 1420, 1419, 1417, 1422, 1424, 1425, 1426, 1428, 1429, 1432, 1440, 1443, 1447, 1449, 1450, 1451, 1452, 1408, 1209, 1212, 1211 (caudal vertebrae).

Series of Cinco Saltos 2: MLP CS 1165, 1139, 1406, 1378 (cervical vertebrae); MLP CS 1376, 1379, 1382, 1383, 1384 (dorsal vertebrae); MLP CS 1389, 1392, 1393, 1399, 1400, 1401, 1413, 1407 (caudal vertebrae).

Series of Cinco Saltos 3: MLP CS 1142, 1375, 1374 (cervical vertebrae); MLP CS 1377, 1371 (dorsals); and MLP CS 1395, 1396, 1397, 1408, 1410, 1421, 1423, 1427, 1430, 1431, 1396, 1465, 1438, 1434, 1433, 1436, 1437, 1439, 1442, 1444, 1445, 1446, 1320 (caudal vertebrae).

Series of Cinco Saltos 4: MLP CS 1398, 1411, 1415, 1622, 2000, 2001, 1441, 1321, 1323, 1207.

Scapula MLP CS 1129, 1096 and MLP Ly 107, (711A).

Coracoids MLP CS 1096, MLP Ly 105, 14, 95.

Humeri MLP CS 1100, 1051, 1091, 1099, 1019, No. 124 (right); MLP CS

1050, 1100, 1479, No 25, No. 89 (left).

Ulnae MLP CS 1058, 1306, 2004 (left) and MLP CS 1305 and 1053 (right)

Radii MLP CS 1172, 1173, 1167, 1169 (right) and MLP CS 1175, 1174, 1176, 1173 (left).

Carpals MLP CS 1234.

Metacarpals (assigned with doubt) MLP CS 1187, 1186, 2003.

Phalanges MLP CS 1261.

Ilija MLP CS 1258, 1257, 1229, 2008, 1056, 1298.

Pubes MLP CS 1263, 1304, 1102, 1294 and No. 109.

Femora MLP CS 1120, 1021, 1107, 1101, 1118, 2005 (left).

Tibiae MLP CS 1093 (right) and MLP CS 1103, 1123 (left).

Fibulae MLP CS 1098 and No. 127.

Tarsals Right astragalus MLP CS 1216.

Metatarsals I. MLP CS 1179, 1185, 1183, 1199; II. MLP CS 1193, 1137, 1238, 1177, 1236; III. MLP CS 1178, 1201, 1197; IV. MLP CS 1191, 1198, 1190, 1189; V. MLP CS 1195, 1181, 1180, 1182, 1184.

Modified diagnosis. Titanosaurids of small and medium size similar to *Saltasaurus loricatus*. Cervical centra short and broad. Short dorsal centra with reduced pleurocoels. Sacrum with six well coossified centra, narrow from the second to the fifth sacral vertebrae. First caudal vertebra

biconvex. Caudal centra rather short and with a very concave ventral face bounded by rounded edges. Scapula with a prominent muscular attachment on the medial face, near the dorsal edge, as in *Saltasaurus loricatus*. Sternal plate with a very prominent ventral crest. Limb bones rather short, but more slender than in *Saltasaurus loricatus*. Radius of sigmoid outline. Short and stout metacarpals. Ilium with preacetabular laminae laterally expanded, but somewhat shorter than in *Saltasaurus*. Fibula with simple but well developed lateral tuberosity. Astragalus transversely short.

Comments

The sacrum MLP Ly 7 should be considered as belonging to the same individual of the holotype. Two caudal centra, MLP Ly 66 and 48, articulate with element MLP Ly 5 of the holotype. Likewise, element MLP Ly 6 should be discarded from the holotype, since it clearly is a caudal centrum of the same species but a different individual. MLP Ly 1 should be excluded from the material corresponding to the holotype as well since its morphology clearly indicates it belongs to a titanosaurid closely related to *Titanosaurus*.

Description

Cervical vertebrae (Pl. 56:2 and 3)

The only part of the centrum of the atlas preserved is that which articulated with the axis (MPL CS 1311). The axial centrum has a convex ventral face with a medial edge resembling the one observed in Titanosauridae indet. (Series A from the DGM of Brazil). Unlike the axis of *Saltasaurus*, it lacks a medial lamina. The parapophyses are flat tuberosities located anteriorly above the anterior edge of the centrum, with a crest turned posteriorly. The ventral face of the anterior-most cervical vertebrae is longitudinally concave. This surface becomes progressively flatter posteriorly in the cervical series. Some of the latter (MLP CS 1366 and 1375) show a pair of vascular foramina near the anterior edge. The anterior surface is markedly convex and broad. Lateral faces are strongly concave and bounded ventrally by the parapophysis, which project laterally and ventrally.

Diapophyses are preserved only in some posterior centra. They project horizontally and laterally from the anterior part of the centra. The diapophysis is directly linked with the prezygapophysis which lies dorsal and anterior to it. Posteriorly there are two laminae: one links the diapophysis with the postzygapophysis and is the equivalent of the horizontal lamina (Osborn 1903). The diapophyseal lamina is the second one and links the diapophysis with the centrum. The neural spine is low, undivided, and somewhat broadened at its dorsal tip which gives it a wedge-shape. The tip of the spine is rounded. Posteriorly, it connects with the postzygapophyseal lamina and shows no postspinal lamina. The prezygapophyses are linked to one another by a relatively thin horizontal lamina which serves as a roof to the neural canal. In addition, there is a prespinal depression between the prezygapophyses. This prespinal

depression is bounded on either side laterally by two laminae that are formed by the division of the prespinal lamina towards the base of the spine. The facets on the pre- and postzygapophysis are subcircular, rather large and somewhat convergent ventrally.

Dorsal vertebrae (Pls 56:1 and 57)

The centrum of the 1st dorsal vertebra is rather short. In the middle of the dorsal series, the centra are longer. The centra are again shorter at the rear of the dorsal series. On the centrum of the anterior dorsal vertebra, the ventral face is flat, a character that changes in the series towards the back. Towards the 3rd dorsal vertebra, the section is cuneiform at the base (Pl. 57:1 and 6). The body of the dorsal vertebrae tend to broaden posteriorly in the series along with a general increase in size. The pleurocoels, short and low on the first dorsal vertebra, become higher towards the 3rd. Posteriorly in the dorsal series, the pleurocoel enlarges and becomes longer. Parapophyses are well developed in front of the pleurocoel in the 1st dorsal vertebra (MLP CS 1357). Posteriorly, this element has a prominent facet with an oval outline. Posteriorly, the parapophysis becomes higher until by about the 6th dorsal vertebra it is at the same height as the prezygapophysis. The prezygapophysis of the anterior dorsal vertebrae (1st and 2nd; Pl. 56) do not possess the pillars which support these structures (double or single), as seen in *Saltasaurus loricatus*. The neural spine has been preserved in a few specimens. In the centra MLP CS 1381 (Pl. 57:3), which probably corresponds to the 4th dorsal vertebra, the neural spine is quite inclined and its system of reinforcing laminae, with a well developed prespinal lamina, is different from that of *S. loricatus*. MLP CS 1373 preserves the base of the spine which is reinforced by the diapophyseal, prespinal and spinal prezygapophyseal laminae. The latter ones are scarcely developed. In MLP CS 1385, the prespinal lamina is very different from *S. loricatus* by being thick and prominent.

Sacrum

Of the holotype, an incomplete sacrum formed by the fused vertebral body and the base of the parapophyses (MLP Ly 7—Pl. 58:5) has been preserved. The anterior articular end is convex, while the posterior is slightly concave, differing in this sense from *Saltasaurus loricatus*, some sacra from Brazil and even some from the Neuquén Group. The first three centra are sacralised dorsal vertebrae. The first has a well defined pleurocoel, rather large and deep. The 2nd and the 3rd sacral have pleurocoels as well, also well defined but progressively reduced in size posteriorly. The centrum of the first sacral vertebra is broadened on both ends, the second is expanded only anteriorly, not so posteriorly, where it is not so obviously fused with the centra of the following vertebrae. In ventral view, from the first to the fifth sacral vertebra, the fusion of the centra becomes more obvious posteriorly, together with a marked reduction of size and becoming particularly narrow and cuneiform in cross section. The incomplete sacrum MLP CS 1097 is poorly preserved, but can be seen to be different from MLP Ly 7

in that its posterior articulation is more depressed. Huene (1929a) has interpreted this difference as the consequence of a compressional deformation. However, another possibility that must be borne in mind is that this specimen might belong to a different species or even genus. The comparison of the concave posterior articular end of the sacrum in *Neuquensaurus* with those of concave articular ends of *Saltasaurus* and other titanosaurids of the Baurú Formation, in Peirópolis, suggests two patterns of fusion of the centra to the sacrum. Normally, there are six fused centra in both types. However, in the case of *Neuquensaurus*, there is an additional dorsal vertebra (tendency to incorporate elements cranially). In the other type the first biconvex caudal vertebra instead of the dorsal vertebra is added to the sacral series (tendency to incorporate vertebrae caudally).

Caudal vertebrae

All the caudals are procoelous, except the first which is biconvex. The rest of the caudals are similar to *Saltasaurus loricatus*, in spite of which they can be easily differentiated. The ventral face of the centrum of the first caudal vertebra is slightly convex. Its length is slightly shorter than that of the last sacral vertebra. On the second? caudal vertebra that ventral face tends to flatten. Beginning with the 3rd caudal vertebra, the large and deep depression characteristic of the species (Pl. 58: 1a, 2a and b; 3a and b; 4) bounded by rounded edges and ending at the articular facets for the hemapophyses, starts to develop. The length of the centra, progressively enlarges, starting at the second caudal vertebra to approximately the ninth *sensu* Huene (1929a). From that point posteriorly, the caudal vertebrae become smaller. From the second caudal vertebra posteriorly, all are procoelous. The articular surfaces of the centrum of the first caudal vertebra are slightly different from one another: the anterior is less prominent and more reduced than the posterior. In the first caudal vertebra, the articular surface has a slightly oval and depressed outline. In the caudal vertebrae immediately posterior, the height is slightly greater than the width while the distal caudal vertebrae are again characterised by being strongly depressed. The transverse process of the first caudal vertebra has an extended base which lies along the lateral wall of the neural arch and extends to a point under the posterior part of the prezygapophysis. Moving posteriorly in the caudal series, the transverse process becomes progressively lower and tends to form a tuberosity that by the sixth? caudal vertebra is located more or less at the articulation between the centrum and the neural arch. The neural arch of the first caudal vertebra is short, and situated above the anterior part of the centrum of the following vertebra. On more posterior caudal vertebrae, the neural arch becomes more elongated. The prezygapophysial facets are large in the first caudal vertebra and become steadily smaller further posteriorly in the caudal series. The prezygapophyses are short in the anterior caudal vertebrae. Posteriorly, they lengthen and turn into a horizontal process. The neural spine, almost vertical and

anteroposteriorly compressed in the anterior caudal vertebrae, tends to bend progressively backwards in a way that towards the ninth caudal vertebra overlaps the postzygapophysis. The most anterior caudal vertebrae exhibit pre- and postspinal laminae. The prespinal lamina is also present in more posterior caudal vertebrae. The spinoprezygapophysial laminae are highly developed. The anterior caudal centra are cancellous as in *Saltasaurus loricatus* although this condition is less developed than in that species.

Coracoid (Pl. 59:4)

The coracoid is not very different to that of *Saltasaurus loricatus*. It has a quadrangular outline, with the medial edge straight and thickened. As in *S. loricatus*, it has a longitudinal elevation parallel to the anteromedial edge that is located above the glenoid articulation.

Scapula (Pl. 59:4)

Among the elements referred to this species, there is a scapula articulated with the coracoid. It shows some resemblances with *Saltasaurus loricatus*, but differs by the possession of a rather narrow lamina on its proximal part, and by the more acute angle between the scapular lamina and the crest that lies along the margin of the supraglenoid depression. The ventral margin of the scapular lamina is straight over its entire length.

Sternal Plates

The sternal plates are flat and broad laminar elements. Their morphology matches with that of *Saltasaurus loricatus* except that the crest on the medial face, close to the upper margin, is far more prominent.

Humerus (Pl. 59:1)

The humerus is more slender than in *Saltasaurus loricatus* and most of the muscular scars are more prominent. The deltopectoral crest is broad and distinct. Huene (1929a) considered as a diagnostic the difference between *Neuquensaurus australis* and *N. robustus* in the absence of a corner in a superolateral right angle, which the latter species possess. However, my own observations lead me to conclude that this difference is of dubious value because the humerus assigned to *N. australis* is generally broken at this place.

Ulna (Pl. 59:2)

The ulnae assigned by Huene (1929a) to this species are straight and quite slender compared to those of *Saltasaurus loricatus*. Some elements, such as MLP CS 1053, have been affected by abrasion at the proximal and distal edges (especially the olecraneal area); the slender appearance of the bone is owing to this. Other specimens such as MLP CS 1058 (Pl. 6:8), are more slender than those of *N. australis*. It seems reasonable to presume that they belong to a juvenile *Titanosaurus* sp.

Radius (Pl. 59:3)

The radius has a somewhat sigmoid outline. The proximal articular end is slightly concave, and the plane that passes

through its edges is perpendicular to the long axis of the bone. Oblique longitudinal crests run over the radial face. These are particularly obvious at the distal ends.

Metacarpals

Some specimens from Cinco Saltos have been identified as metacarpals. Among others, are MLP CS 1197/1189/1238. They are relatively short and stout in comparison with those of *Titanosaurus araukanicus* and *Antarctosaurus wickmannianus*, closer in that sense to *Saltasaurus loricatus*. Huene (1929a) identified these metacarpals as metatarsals, since he thought that metatarsals should be considerably longer, as in other known genera (*Antarctosaurus* and *Argyrosaurus*).

Ilium

The preacetabular part of the iliac lamina is curved laterally, but is less extended than in *Saltasaurus*. The pubic peduncle is transversely broad. The acetabulum has a parabolic outline in lateral view, with the apex at the junction of the pubic articulation with the iliac lamina. The iliac ischiatic articulation is not located on a prominence, but on a broadening of the iliac lamina. None of these specimens has been preserved in their entirety.

Pubis

The pubis resembles that of *Saltasaurus loricatus*. However, it is somewhat narrower and has a smaller obturator foramen 1.5 cm in diameter. The distal part of the lamina is broad, with no pronounced thickening. The lateral edge of the lamina is somewhat thick, but the medial edge is not.

Ischium

The distal part of the ischium is laminar and lacks an expansion. On the proximal part, the thickening corresponding to its articulation with the ilium is apparent. The articular surface for the pubis is separated from articulation for the ilium by the concave surface which corresponds to the ischiatic region of the acetabulum.

Femur (Pl. 60:3 and 6)

The femur is a straight bone flattened anteroposteriorly as in all titanosaurids. The femur MLP CS 1122, was included by Huene (1929a) among the specimens referred to *Neuquensaurus australis*. However, a comparative study of the specimen shows that it probably belongs to a juvenile of *Titanosaurus* sp. (Pl. 60:1 a and b).

Tibia

Like the femur, the tibia lacks clear diagnostic features, except for its general proportions. It differs from *Saltasaurus loricatus*, and the type of *Titanosaurus robustus* in being more slender. However, this apparent difference is worthless because some of the elements are affected by abrasion, giving them a look of accentuated grace.

Fibula (Pl. 60:4 and 5)

As with the fibula of *Saltasaurus loricatus*, the fibula has a simple lateral tuberosity. However, the tuberosity is far more protuberant, and better defined. The morphology of the lateral tuberosity is quite different from those in *Antarctosaurus*, *Argyrosaurus* and *Titanosaurus*.

Tarsus

The astragalus is a transversely short bone. Its fibular articular surface is concave and quite vertical, while the tibial face is far broader and less sloped than the former. Huene (1929a) describes what he thought to be a calcaneum (MLP CS 1233) but there is no evidence to support this interpretation. According to Romer (1956), the calcaneum did not ossify in sauropods. A specimen found in the Nuequina Basin represented by the tibia and an articulated astragalus, with remains of the fibula adhering to both bones (MPCA 1235), permits the reconstruction of this articulation. Based on this specimen, there may have been a bony element such as the calcaneum ventral to the fibula. Such a bone would have been shorter than the astragalus. Huene (1929a) considered as a calcaneum a bone half the height of the astragalus which would have been reasonable.

Finally, until new evidence is available, it should be considered as a strong possibility that titanosaurids had an ossified calcaneum.

Comparisons

Neuquensaurus australis is a form close to *Saltasaurus loricatus*, resembling it mainly in the size of its adult forms (small to medium), morphological traits, the proportions of the limb bones and general characteristics of the vertebrae. Although the dorsal vertebrae are not well preserved, because they generally lack diapophysis, clear differences can be seen in the architecture of the different specimens. The preserved parts of the dorsal vertebrae have a pattern resembling *S. loricatus*. However, the few neural spines of the dorsal vertebrae preserved show that its system of reinforcing the laminae is somewhat different to that of *S. loricatus*, with a larger development of the prespinal laminae. The sacrum is opisthocelous, a detail that differentiates it from *S. loricatus*, where sacralization is evident in the first biconvex caudal vertebra, resulting in a biconvex sacrum. The general form of the caudal vertebrae is close to *S. loricatus*, although it clearly differs in the morphology of the ventral, which in *Neuquensaurus* is a wide, undivided, deep depression. The anterior and medial caudal vertebrae of *S. loricatus* normally show a narrower ventral depression with a medial crest. The limb bones are commonly more slender than in *S. loricatus*.

Some bones assigned by Huene (1929a) to *Neuquensaurus*, could, as formerly stated, belong to *Titanosaurus* sp. juveniles. The scapula of *Neuquensaurus* shares the same medial projection close to the dorsal edge as *Saltasaurus* and *Aeolosaurus*, differing in this way from *Titanosaurus araukanicus* and *Antarctosaurus wickmannianus*.

The metacarpals are short and stout as in *Saltasaurus* rather than relatively slender as in *Titanosaurus* and *Antarctosaurus*. In spite of the difference in size, the relative proportions of the metacarpals resemble those of *Aeolosaurus* and *Argyrosaurus*.

The differences between *Neuquensaurus* and *Titanosaurus araukanicus* are similar to those pointed out between *Saltasaurus* and the latter.

Aeolosaurus rionegrinus, although bigger in size, shares with *Neuquensaurus australis* the stoutness of the limbs, short metacarpals, simple lateral tuberosities, and a scapula with a process for a prominent muscular attachment, on its dorsal edge. However, they clearly differ, because *Aeolosaurus* has caudal vertebrae that are definitely titanosauriform.

A detailed analysis of the anatomical characteristics of the caudal vertebrae of this form, originally described by Lydekker (1893) as *Titanosaurus australis*, provides the basis to conclude that it belongs to a genus other than *Titanosaurus*. In any case, it is closer to *Saltasaurus loricatus*. However, its differences from *S. loricatus* justifies the recognition of *Neuquensaurus* as a distinct taxon as proposed by Powell (1992).

Taphonomic characteristics

The specimens referred to this species were collected from strata consisting of accumulations of disarticulated bone remains, where specimens were found which belong to different individuals of the same species and a mixture of other genera, or isolated remains found at different sites which certainly seemed to have been transported before burial.

In the case of the specimens studied by Lydekker (1893), these were obtained from the Río Colorado Formation (Bajo de La Carpa Member) near the city of Neuquén. In addition to this collection, Huene (1929a) based his studies upon an ample collection from Cinco Saltos (the lower member of the Allen Formation), General Roca (Anacleto Member of the Río Colorado Formation) and Rancho de Avila.

Collecting methods

The specimens studied by Lydekker (1893) were collected for Santiago Roth of the Museo de La Plata and possibly before, by soldiers between 1882 and 1887 (Huene 1929a). These specimens were found on the surface and there is no data available concerning the characteristics of the strata and the possible association between the specimens, except in a few cases where it is possible to fit pieces of the same specimen together.

The material from Cinco Saltos was collected from a number of different places by personnel from the Museo de La Plata. There is no data concerning the exact location or rough sketches to reconstruct associations between these specimens collected.

Procedures of the taxonomic work

In his study on the Cretaceous dinosaurs of Patagonia, Lydekker (1893) grouped the similar available specimens according to the limited available knowledge and on the basis of his experience, there being no collection data.

Subsequent analysis of the collections at the Museo de La Plata indicates that among the material Lydekker (1893) based the species *Titanosaurus australis* upon, included the specimens here considered to be *Neuquensaurus australis*, together with fossils belonging to other individuals as well as other genera. In that same work, Lydekker refers to that species' femora, a humerus and a dorsal vertebra, which very probably belong to *Titanosaurus sensu stricto*.

Huene (1929a) revised the specimens studied by Lydekker, and moreover brought together an important collection of elements according to their form. He classified the long limb bones as either slender or robust, and called them *Titanosaurus australis* and *Titanosaurus robustus* respectively. He did this without determining or differentiating the vertebral material of each species. In other words, Huene (1929a) used the name of *Titanosaurus australis* in an arbitrary way to identify the form possessing slender limb bones and creating for the remainder the species *T. robustus*, without taking into account the fact that the type material of the species *T. australis*, which as already noted, consists of a series of caudal vertebrae. In light of the basis for differentiating between *N. australis* and *N. robustus*, and the likelihood that the greater part of the differences between them correspond to individual variations, in the present work it is proposed to consider *Neuquensaurus australis* as a valid species, while regarding *N. robustus* as *nomeu dubium*. This position is provisional and undoubtedly could be confirmed or refuted with the discovery of an articulated or an associated skeleton of a single individual.

One of the specimens assigned by Huene (1929a, p. 301) to *Titanosaurus australis* belongs, according to this author, to a sauropod outside of the Titanosauridae and undoubtedly older. This specimen comes from Alarcon on the left bank of Río Limay, and was described by Nopsca (1902). Among the most compelling characters supporting this interpretation is the markedly reduced vertebral body, the wide and deep development of the pleurocoels and the morphology of the neural spine with prominent pre- and postspinal laminae, as well as very noticeable laterally oriented diapophyseal laminae. Hatcher (1903) points out the resemblances of these vertebra with those of *Haplocanthosaurus*. Probably this material is from the Early Cretaceous outcrops of this region which have yielded other sauropod specimens.

Neuquensaurus robustus (Huene 1929a).

Nomen dubium

Plates 59:2, 3 and 6; 60:2-4)

Titanosaurus robustus Huene 1929a, p. 48; Plates 18-21; Steel 1970, p. 77; Bonaparte 1978, p. 555; Pl. 265r; Bonaparte and Gasparini 1979, p. 397; Olshevsky 1978, p. 28.

Lectotype. MLP CS 1095 (right and left ulnae), MLP CS 1171 (left radius) and MLP CS 1480 (left femur) - (Bonaparte & Gasparini 1979).

Locality. The region of Cinco Saltos (lectotype) and Rancho de Ávila, Province of Río Negro (Huene 1929a).

Stratigraphic position. Lower member of the Allen Formation and the Río Colorado Formation of the Neuquén Group (in Bonaparte & Gasparini 1979).

Specimens referred to the species. These are the specimens of this species listed by Huene (1929a): MLP CS 1139/1165/1406/1378 (cervical vertebrae); MLP CS 1376/1379/1382/1383/1384 (dorsal vertebrae); MLP CS 1295 (left sternal plate); MLP Av 2064 (scapula); MLP CS 1019 (humerus); MLP CS 1091/1095/1094/1052 (ulnae); MLP CS 1171 (radius); MLP Av 2069/2068/2083/2169 (ilia); MLP Av 2066 (pubis); MLP 1125/MACN 'drawer 563' (femora); MLP CS 1264/1303/2064 (tibia); MLP CS 1184/1179 (phalanges).

At present it is impossible to decide if the specimens listed here belong to a single individual. It is very probable that a large part of these specimens belong to *Neuquensaurus australis*, while the others could actually belong to other genera and species.

Description

The lectotype designated by Bonaparte and Gasparini (1979), include a pair of ulnae (left and right), a left radius and a left femur.

Ulna (Pl. 59)

The ulna is relatively short, very robust, with the proximal end very expanded. Its radial face is deeply concave. The posterior face is longitudinally concave, owing to its proximal expansion, which results in an arched posterior outline.

Radius (Pl. 59:3)

The radius is a stout bone, expanded at its proximal end, where the anterior projection of the articular surface expands in a more obvious manner than in *Neuquensaurus australis*. The diapophysis is apparently stouter than in *N. australis*, resembling more that of *Saltasaurus loricatus*.

Femur (Pl. 60:3 a and b)

The femur is not very different from MLP CS 1118, assigned by Huene (1929a) to *Neuquensaurus* (= *Titanosaurus*) *australis*, except that in the lectotype of *N. robustus*, the 'step-like arrangement' between the trochanter major and the articular heads is more evident. The rest of the general characters resemble *N. australis*.

Comments

In the discussion of the *Neuquensaurus australis*, the methodology used by Huene (1929a) to distinguish it from *Neuquensaurus robustus* on the basis of the proportion of the limb bones without consideration of the type material of *N. australis*, which he could not with certainty assign to either species is outlined. Although specimens arbitrarily assigned to *N. robustus* show some differences of probable taxonomic value, in many cases the differences are just a matter of preservation or comparison with different genera. It is also necessary to consider that the differences are simply individual variation or owing to sexual dimorphism.

Without completely discounting the possibility that in the upper levels of the Neuquén Group and in the Malarque Group there were contemporaneous species of similar size and morphology, which lived together, in the present paper *Titanosaurus robustus* is considered as *nomen dubium*.

Genus *Microcoelus* Lydekker 1893

Nomen dubium

Microcoelus Lydekker 1893, pp. 12-13; White 1973, p. 140.

Type species. *Microcoelus patagonicus* Lydekker 1893.

Distribution. The same as for the type species.

Microcoelus patagonicus Lydekker 1893

Nomen dubium

Plate 7, la and b

Microcoelus patagonicus Lydekker 1893, pp. 12-13, Pl. 3:2

Holotype. MLP Ly 23. An incomplete anterior dorsal vertebra.

Locality. Right bank of the Río Neuquén, between 2 and 4 km upstream from the railroad bridge which crosses the river, very close to the city of Neuquén.

Stratigraphic position. Río Colorado Formation, Bajo de La Carpa Member? (Neuquén Group).

Age. Late Cretaceous. Campanian (Uliana & Dellapa 1981).

Description

The holotype is a small centrum which probably belongs to a first or second anterior dorsal vertebra. In ventral view, the centrum is broad and lacks a keel. The parapophyses are located slightly in front and above the pleurocoel. Part of the neural arch has been preserved.

Comments

The specimen upon which this taxon is based provides no valid diagnostic features by which it can be referred to any known titanosaurid taxa. For this reason, I consider *Microcoelus patagonicus* as a *nomen dubium*. Lydekker

(1893) assigned to this same species a humerus which most probably belongs to *Neuquensaurus australis* (Lydekker 1893: Pl. 4:2a and 2b). Huene (1929a) included the type, and another specimen referred to *M. patagonicus* among the material which he assigned to *Neuquensaurus* (= *Titanosaurus*) *australis*, which is probably correct. The general morphology and proportions of the available material allow its assignment with relative certainty to the Subfamily Saltasaurinae.

Genus *Antarctosaurus* Huene 1929a

Antarctosaurus Huene 1929a, p. 85; Huene 1956, p. 510; White 1973, p. 121, Van Valen 1969, p. 169; Steel 1970, p. Olshevsky 1978, p. 28.

Type species. *Antarctosaurus wichmannianus* Huene 1929a

Distribution. Late Cretaceous. Senonian Pre-Maastrichtian of Río Negro Province and Neuquén, Argentina, Brazil? and India?

Provisional Diagnosis. Femur straight and slim, cranial articulation vaulted, fourth trochanter somewhat above the middle of the bone. The characters of the cranium and post-cranial skeleton are only known in *Antarctosaurus wichmannianus* Huene 1929a.

Antarctosaurus wichmannianus Huene 1929a
Plates 62, 63, 64, 65: 11, 12 and 13

Antarctosaurus wichmannianus Huene 1929a, pp. 66–67, pls 28–34, 35: 1–9; Steel 1970, p. 75; Bonaparte 1978, pp. 560–561; Bonaparte and Gasparini 1979, pp. 400–401; Olshevsky 1978, p. 27.

Holotype. MACN 6904. Incomplete cranium and mandible, rib fragments, left scapula, incomplete right humerus, two fragments of the distal radius, a fragment of the proximal end of an ulna, seven metacarpals (two of these incomplete), a phalanx, a fragment of an ilium, almost complete right ischium and part of the left, a fragment of the pubis, left femur, left tibia, left fibula, five left metatarsals and some phalanges from the foot.

Locality. Fifteen kilometres to the south-west of the city of General Roca, El Cuy Department, Río Negro Province.

Stratigraphic position. Anacleto Member? Río Colorado Formation. Neuquén Group (Bonaparte & Gasparini, 1979).

Age. Senonian pre-Maastrichtian, Campanian? (Uliana & Dellapa 1981).

Specimens referred to the holotype. Only those of the holotype.

Diagnosis. Straight and slender femur, massive rounded articular head. Fourth trochanter slightly above the midpoint of the bone. Skull and postcranial skeleton characters only known in *Antarctosaurus wichmannianus*, Huene 1929a, which should be considered for the present as diagnostic of the genus.

Modified diagnosis. High skull at the back, large orbits; wide muzzle, straight and broad symphyseal region perpendicular to the mandibular rami. Parietal and frontal broad, and short. Upper temporal fenestra reduced but partially open towards the dorsal side. Triangular basi-presphenoid complex wide and short. Foramen for nerves IX–XI separated from the fenestra ovalis. Basipterygoid process long, in the form of a bar and very divergent. Basioccipital tuberosities separated. Paroccipital processes long and recurved as in *Saltasaurus*. Narrow scapular blade; wide supraglenoid regions. Axis of the lamina almost perpendicular to the major axis of the supraglenoid part of the scapula. Ischiadic lamina narrow, distally expanded. Well developed pubic peduncle. Tibia with stout articular ends. Fibula with lateral tuberosity formed by two parallel rugosities that are parallel to the long axis of the bone.

Description

Skull (Pls 62, 63 and 64)

Posteroventral view

As illustrated by Huene (1929a) *Antarctosaurus wichmannianus* had long and recurved paroccipital processes, similar to those seen in *Saltasaurus loricatus*. This part of the skull has not been preserved in the specimen available at the Museo Nacional de Ciencias Naturales 'B Rivadavia'. The occipital condyle is large and rounded. Beneath it are located the basioccipital tuberosities which are separated from one another by a smooth groove. The supraoccipital prominence clearly stands out on the cranial roof. Over the exoccipitals is the opening for nerve III, corresponding to that indicated as 'V' by Huene (1929a; Pl. 28: I). In contrast to *S. loricatus*, the prominences on both sides of the foramen magnum are hardly noticeable. Although sutures are not visible, it can be inferred that the occipital condyle is totally formed by the basioccipital, except some small ventrolateral parts which could be formed by the exoccipitals.

Lateral view (Pls 64c and d; 63)

The orbitosphenoids and laterosphenoids are totally fused, rendering the suture between them invisible. In contrast, the suture of this complex with the frontal is very clear. The opening of nerve IV (Trochlear) is above and behind the point of emergence nerve II (Optic). The opening for nerve III (Oculomotor) is immediately below that for nerve IV, and has the shape of an '8'. Nerve III probably emerged from the dorsal part of the oculomotor foramen while the ventral part could correspond to a non-ossified part of the lateral wall of the pituitary fossa. Below and behind the pituitary fossa is the opening for nerve VII (Facial) which has a diameter of 4 mm.

Nerve V (Trigeminus) emerges from the skull through an opening located just under the *crista antotica*. The *crista prootica* is the basal part of the posterior wall of the upper temporal fossa. Behind the *crista antotica*, there is a depression in which there are two openings: the anterior being the *fenestra ovalis* while the posterior is the foramen for nerves IX–XI. Both openings face laterally

and ventrally and have canals which continue ventrally. The morphology of this sector clearly differs from that of *Saltasaurus loricatus*, in which there is just one external opening for the *fenestra ovalis* and nerves IX–XI.

Cranial roof (Pls 63 and 64c)

There is a longitudinal prominence on the sutural contact between the two frontals. The supratemporal opening extends to the limit of the lateral or orbital region, with the medial region of the frontal being much more developed than in *Saltasaurus loricatus*. *Antarctosaurus wichmannianus* does not have the marked depression present in *S. loricatus* which is located on the anterior edge of the parietal and the anterior margin of the parietal wing. The supraoccipital tuberosities are rounded and terminate in a smooth apex.

Floor of the braincase (Pls 62b and 64f)

The pituitary fossa is deep. The basipresphenoid complex forms a triangular concave facet, with a broad base on the occipital side. This character marks a strong difference with *Saltasaurus*, which has a triangular and narrow-based basipresphenoid complex and, instead of a broad facet, a strong sagittal crest.

Quadrate

The proximal end of the right quadrate has been preserved in articulation with the squamosal, and the left quadrate, preserved as an isolated but almost complete bone. In the dorsal region, a small shaft, recurved laterally and posteriorly terminates on the rounded articular facet for the squamosal. An expansion is formed by two ventrally joined laminae along the medial edge which delimit a wide 'pocket' with a laterally and posteriorly oriented opening. Most of the posterior lamina is lost, especially in the area close to the medial edge of this 'opening'.

Squamosal

The left squamosal is unknown. The right squamosal is almost complete. It articulates with parts of the postorbital and quadrate. The lateral margin of the upper temporal fossa is formed by the squamosal, which is oriented somewhat dorsally rather than dorsally and laterally, as in *Diplodocus*. There is a posterolaterally facing triangular surface on the squamosal which probably served as site for muscular attachment. This surface is continuous with those of the parietal wings. The lateral face of the squamosal is rather flat. Posteriorly, it is prolonged as a laminar apophysis which, if complete, would have its apex at the height of its articulation with the quadrate.

On the medial face there are two depressions: an anterodorsal one, very wide, which forms the roof of the infratemporal fossa; the other separated from the former by a high and sharp crest, in which fits the dorsal region and dorsal articulation of the quadrate. The posteroventral margin of the infratemporal opening is formed by the ventral projection of the squamosal, which although not

completely preserved, is nonetheless longer than in *Diplodocus*.

Postorbital

A partial right postorbital is available. It has a triangular cross-section. The lateral face is relatively flat, while the anterior is concave, in both the transverse and the longitudinal dimension, in relation to the bone's axis, forming as it does the posterior part of the orbit. Along the medial face it articulates with the squamosal. The bone is incomplete ventrally and dorsally.

Jaws

An almost complete right ramus is available, with only part of the symphyseal region missing. It has a very peculiar morphology since it is low over its entire length, and rather thick. The symphyseal region forms an almost vertical wall, scarcely bent forward, while in the anterolateral corner, which forms a right angle, the dorsal or alveolar region is turned anteriorly and laterally, tending again to form a vertical plane towards the condylar region. The symphyseal region is wide and straight. It has 15 alveoli confined almost completely to the symphyseal region as in *Diplodocus*. On a partial jaw which probably consists of the angular and surangular are attached fragments of the splenial and coronoids (Huene 1929a).

Teeth

Some of the alveoli show erupting teeth. Attached to the anterior wall of the symphyseal region of the left dentary ramus are three complete teeth, which are the basis to characterise its morphology. They are buccolingually flattened cylinders with a pointed apex that show no sign of wear.

They are smaller than those of cf. *Titanosaurus* (Powell 1979), reaching a preserved length of 2.3 cm. Their diameter at the root is 4 mm.

Postcranial skeleton

The left scapula of *Antarctosaurus* (Pl. 65:13) is almost completely preserved. The scapular lamina is relatively narrow and forms almost a right angle with the major axis of the proximal expansion of the scapula. The latter region is quite tall, and the depressed supraglenoid area is wider than in *Titanosaurus*, *Neuquensaurus* and *Saltasaurus*.

The scapula of *A. wichmannianus* shows no prominence on the dorsal edge such as in *Neuquensaurus*, *Saltasaurus* and *Aeolosaurus*.

There is a poorly preserved and incomplete right humerus. The medial part of the diaphysis and all the medial edge is missing. The near absence of important morphological traits, makes comparative work difficult. As a consequence, the humerus is of dubious diagnostic value.

Only terminal parts of the ulna and radius are known.

They do not have valuable diagnostic features. For additional information see Huene's (1929a) monograph.

Metacarpals II to V of both sides have been preserved, as well as the proximal half of I?. The proximal ends were articulated, making a fluted structure (Huene 1929a) as in *Alamosaurus* and *Argyrosaurus*. As in those genera, the articular facets of the proximal end of metacarpals II, III and IV are triangular, with the apex ventrally directed. Although there are differences in detail, in general the proximal articulation is the same.

Only the posterior part of the left ilium has been preserved. The articulation of the ischium is visible together with part of the articular surface of the acetabulum. Behind the articulation of the ischium, the lamina projects slightly posteriorly. The dorsal edge of the ilium, with the rugosity for the muscular attachment of the iliotibial muscle, has been preserved.

The distal part of the right pubis has been preserved. The pubic lamina reaches a width of 32 cm with a thick distal end.

A fragment of the left ischium has been preserved with what appears to be the medial edge of the lamina together with its articulation to the ilium but lacking its distal end. Some of these details may be incorrect. The ischium of *A. wichmannianus* is narrower and the lamina relatively long compared to those of *Neuquensaurus* and *Alamosaurus*.

The femur (Pl. 65:12) is flattened anteroposteriorly. The diaphysis is straight and slender. The articular head projects inwards and has, as typical of the large sauropods, a flattened facet in the direction of the long axis of the bone, and strongly convex facet in the transverse plane. Located near the medial edge of the femur, the reduced fourth trochanter protrudes beyond the posterior face of the bone. It is located near the midpoint of the bone's length.

The tibial ends are stout and the diapophysis is flattened. These features are accentuated by deformation. The proximal articular surface is roughly triangular with the proximal depression located on the fibular side. The distal condyles are greatly expanded as in *Saltasaurus loricatus* and *Neuquensaurus australis*.

The right fibula (Pl. 65:13) is almost completely preserved, although it is quite deformed. The posterodorsal corner is missing, as well as the medial part of the posterior edge. From the diagnostic point of view it is one of the most useful elements of the postcranial skeleton. It is long and slender, with its outline very affected by the previously mentioned deformation. As pointed out by Huene (1929a), the most outstanding trait is located on its lateral face: two parallel swells which approximately parallel the long axis of the bone. This sort of lateral tuberosity differs from those in *Titanosaurus* and *Saltasaurus*, resembling partially those of *Argyrosaurus superbus*?

The left metatarsals I to IV have been preserved, and possibly metatarsal V. They are short and stout, with their proximal ends showing opposition surfaces for articulation with the adjacent metacarpals.

Comparisons

As far as the cranium is concerned, its preservation and characters allow the detailed analysis of a number of outstanding differences. Unfortunately, titanosaurid cranial remains are very rare, and of the few available for direct comparison, only those of *Saltasaurus* may be of use, since *Antarctosaurus septentrionalis* (Huene & Matley 1933) is poorly preserved. Available plates and descriptions fall short for an effective comparison. A re-examination of these materials is needed.

Other known cranial elements are not directly comparable owing to the fact that the elements in question are not represented in *Antarctosaurus wichmannianus*. Such is the case of *Caupylodoniscus* (Huene 1929a), based on a maxilla, and cf. *Titanosaurus* sp. (Powell 1979) from which a premaxilla is known.

As far as the cranium, *Antarctosaurus* shows some similarities with *Saltasaurus*, which allows its placement among titanosaurids. The long paroccipital processes that both possess, are a unique character among sauropods and even saurischians. There are some striking differences in the cranial morphology that seem to point this genus as primitive in relation to *Saltasaurus loricatus* and probably to *Neuquensaurus australis* which deserve comment. The basiptyergoid processes being in the form of slender cylindrical bars as are present in *Antarctosaurus wichmannianus* is a common feature among sauropods. This suggests that the 'L'-shaped laminar processes present in *S. loricatus* is a derived character.

The incoming foramen of the internal carotid is placed lateral and posterior to the pterygoid processes, in a manner similar to *Diplodocus* (Berman & McIntosh 1978). This is different from *Saltasaurus* which has a more derived condition. The basipresphenoidal complex of *Antarctosaurus* is quite different from that of *Saltasaurus*. Finally the supratemporal opening is directed upwards in contrast to *Saltasaurus* in which this opening is dorsally closed, which is the derived condition. Besides the cranium which shows numerous diagnostic characters, the scapula and the fibula are second in importance, and similarly, the metacarpals.

The femur, although quite complete, shows no characters of importance, the only striking features being the position of the fourth trochanter near the medial edge and the transversely convex facet of the articular head.

The scapula of *Antarctosaurus wichmannianus* is clearly different from those of the other known genera of the family Titanosauridae. *A. wichmannianus* differs from *Argyrosaurus*, *Saltasaurus*, *Neuquensaurus* and *Titanosaurus atankaicus*, by existence of a relatively

narrow scapular lamina in relation to the well developed proximal expansion of the scapula, the two forming a right angle relative to one another. Otherwise, *A. wichmannianus* resembles *T. araukanicus* and *Argyrosaurus* in the absence of a medial muscular attachment on the narrowest part of the scapula and on its inner face near the anterodorsal edge, while differing from *Aelosaurus*, *Neuquensaurus* and *Saltasaurus*, which possess this muscular attachment.

The fibula, with its lateral tuberosity formed by two parallel rugosities, overall resembles the morphology of *Argyrosaurus*. Nonetheless, it clearly differs from the fibula in saltosaurines and titanosaurines.

Comments

As it has been pointed out in Chapter IV, remains of *Antarctosaurus wichmannianus* were found and excavated by Wichmann, who published on them in 1916. The material was obtained at a clearly identified level, and associated with other fossils attributed to *Titanosaurus araukanicus* Huene (1929a). They are at the Argentine Museum of Natural Sciences Bernardino Rivadavia. No plans or notes relating to this site were found which would allow us to know something about the condition and the degree of association of the material, so it is not possible to verify if the postcranial elements that Huene (1929a) included as being *A. wichmannianus* belongs to the same specimen as the skull allocated to that species.

The comparison in *Saltasaurus loricatus* and *Antarctosaurus wichmannianus* of the indices for maximum dorsal breadth of the skull at the level of the orbit relative to the length of the femur shows that the cranium in the latter species is small in comparison to the height suggested by the postcranial elements. This being so, it could belong to a different individual or taxon. On this basis, assuming that the cranial remains of this species belong to adult individuals, they presumably belong to the forms with the largest femurs recovered at El Brete site.

Nonetheless, this might be a misleading comparison because *Saltasaurus* is a particularly short and stout sauropod, and capable of bearing a relatively larger cranium than larger dinosaurs.

It is highly probable that Huene had strong reasons to make such an association because he had the opportunity to communicate with the discoverers of the fossils as well as the opportunity to see photographs of the site that are now lost.

Because it is highly probable that the cranium is associated with the rest of the skeletal material assigned to *Antarctosaurus wichmannianus*, it should be pointed out that this genus until recently was considered as one of the better known of the family, so much so that White (1973) proposed to use this genus as the type for a family which Olshevsky (1978) subsequently did, designating it the 'Antarctosauridae'.

In the present work it is considered that Lydekker's (1893) original nomination of *Titanosaurus* as the type for the family should be maintained, since it is based on fundamental although a limited number of diagnostic characters, and the Titanosauridae is deeply rooted in palaeontological literature.

Unfortunately, in *Antarctosaurus wichmannianus* the long bones of the fore limb are very incomplete and poorly preserved in a way which makes them useless for diagnosis or comparison. For this reason it is not considered appropriate to assign to this genus specimens based solely on isolated elements such as the humerus; e.g. as Casamiquela et al. (1969) allocated to *Antarctosaurus wichmannianus* fragmentary materials such as the proximal end of a humerus.

There remains a certain amount of doubt concerning the tarsal bones of which Huene (1929a) described two: astragalus and calcaneum. It should be mentioned that the calcaneum has not been documented in sauropods which led Romer (1956) to infer that it was not ossified. In this particular case, the specimen illustrated and described as a calcaneum could well be an astragalus of a smaller individual. In the same way, the astragalus assigned to the holotype individual seems to be far too small relative to the tibia, its breadth is only half the distal diameter of the tibia.

Antarctosaurus giganteus Huene 1929a

cf. *Antarctosaurus giganteus* Huene 1929a, pp. 75–77, pls 35 and 36; Van Valen 1969, p. 624; Steel 1970, p. 75; Bonaparte 1978, 1979, pp. 401–402.

Holotype. MLP 26-316. Two femora, two fragments of a pubis, the distal end of a tibia, indeterminate fragments and two incomplete caudal vertebrae.

Locality. Aguada del Caño, 15 km to the north of China Muerta. Huene (1929a). Department of Confluencia, Neuquén Province.

Stratigraphic position. Río Neuquén Formation, Plottier Member. Pascual et al. (1978).

Age. Late Cretaceous, Senonian pre-Maastrichtian. A Campanian age has been inferred for the Río Colorado Formation, which overlies the Río Neuquén Formation, thus raising the possibility of an age much older than Late Campanian for these levels.

Specimens referred to the species. Only the holotype.

Diagnosis. Femur much longer than in the rest of the titanosaurids and more slender than in *Antarctosaurus wichmannianus*. Posterior expansion relatively narrow. Fourth trochanter prominent and situated near the middle of the bone. Caudal vertebrae short, with a broad and convex ventral surface.

Description

The femur is long and slender. Its proximal end is not very broad in comparison with that of titanosaurids that

have long and robust bones such as in *Saltasaurus*, *Neuquensaurus* and *Argyrosaurus*.

The quite prominent fourth trochanter is located near the middle of the femoral length. The articular condyles are well developed, continuing a little close to the diaphysis, with pronounced heights.

Two incomplete pubes are known, of which the left is best preserved. The lateral edge is thick and the medial, thin. The distal end is thickened to a maximum of 14 cm. The proximal end has not been preserved on either of the two available specimens. Two incomplete caudal vertebrae were described (Huene 1929a), they have not been illustrated. He says the centra are short, with the ventral surface of the centrum broad and transversely convex, except for a smooth medial depression 5 cm wide. The posterior dorsal articular surface is much smaller, forming a sharply pointed cone.

Comparisons

Unfortunately *Antarctosaurus? giganteus* is based on only a few specimens and of those, only the femora are complete enough to be relatively useful in taxonomic work.

The slender character of the femur of *Antarctosaurus? giganteus* and its modestly expanded articular ends differentiates it from *Antarctosaurus wickhamianus*, *Argyrosaurus* and the saltasaurines. The adults of the saltasaurines, on the other hand, are notably smaller than the other South American titanosaurs. The slenderness of the femur agrees very well with the titanosaurines, except *Aeolosaurus rionegrinus*.

As Huene (1929a) pointed out, the relative position of the fourth trochanter is similar in *Antarctosaurus*, which, because of the diagnostic value of this character, made this author refer it, with doubt, to this genus. In any case, it is highly possible that the resemblances to *Antarctosaurus* on one side, and with most of the titanosaurids on the other, are isolated convergences instead of indicative of real affinities, because the materials come from different places, and stratigraphic levels.

Comments

Antarctosaurus giganteus is characterised by its colossal dimensions, which is obvious in the size of its femora. Van Valen (1969) considered that this form, together with *A. wickhamianus*, were different stages of the same species, so he proposed the name *A. giganteus* for both. This was rejected by Bonaparte and Gasparini (1979) based on obvious morphological differences, in addition to their having come from different stratigraphic units.

In the present work, following Bonaparte and Gasparini (1979), *A? giganteus* is considered a valid species. Nonetheless, superficial resemblance to other titanosaurids might be owing to convergence. It is highly

probable that this species corresponds to a new genus, although probably to adequately establish its position at the generic level requires the availability of new material which would allow a more thorough knowledge of the skeleton.

Antarctosaurus brasiliensis Arid and Vizotto 1971
Nomen dubium

Antarctosaurus brasiliensis Arid and Vizotto 1971, p. 298, figs 1–7; Bonaparte 1978, p. 561; Olshevsky 1978, p. 27.

Holotype. FFCL GP-RN 2. Incomplete left femur. FFCL GP-RD 3. Incomplete right humerus. FFCL GP-RD 4. Incomplete dorsal vertebra.

Locality. Ruta Estatal Barretos-São Jose do Rio Preto, distance to this locality, 5 km.

Stratigraphic position. Baurú Formation (Arid & Vizotto 1971).

Comments

The species is based on well preserved although incomplete, material from a dorsal vertebra, a femur and a humerus. Preserved on the vertebra are the centrum and neural arch but the apophysis is missing. It shows a reduced pleurocoel, somewhat elliptic in outline.

Only two-thirds of the proximal end of the humerus has been preserved, along with the distal two-thirds of the femur.

The amount of material studied by Arid and Vizotto is insufficient either to establish a new species or to allocate it with confidence to the genus *Antarctosaurus* because there are no known dorsal vertebrae for *Antarctosaurus wickhamianus* or *Antarctosaurus giganteus*.

In addition, the morphologic features of the humerus, as well as the distal part of the femur are not diagnostic as far as the author is concerned.

The available elements are insufficient to assign these remains to any of the known genera of the Titanosaurid family, therefore *Antarctosaurus brasiliensis* is considered as *nomen dubium*.

Genus *Argyrosaurus* Lydekker 1893

Argyrosaurus Lydekker 1893, p. 9; Huene 1929a, pp. 77 and 86; Huene 1956, p. 511; Steel 1970, p. 75; White 1973, p. 122.

Type Species. *Argyrosaurus superbus* Lydekker 1893

Distribution. Late Cretaceous-Senonian of Chubut Province.

Diagnosis. The same as for the type species.

Argyrosaurus superbis Lydekker 1893

Argyrosaurus superbis Lydekker 1893, pp. 9–12, Pl. 37; Steel 1970, p. 76; Bonaparte 1978, pp. 597–58, Fig. 266; Olshevsky 1978, pp. 6–7; Bonaparte and Gasparini 1979, p. 398.

Holotype. MLP 77-V-29-1. Anterior left limb which include a humerus, radius, ulna, carpals and five metacarpals.

Locality. Left bank of the Río Chico, near Pampa Pelada to the north-west of Lake Colhue Huapi (Huene 1929a).

Stratigraphic position. Possibly the Bajo Barreal Formation of the Chubut Group. Bonaparte and Casparini (1979).

Age. Late Cretaceous, probably Senonian.

Material referred to the species. The holotype plus a group of specimens also collected in the San Jorge Basin that are referred to the genus and with doubt to the species, and are discussed and described below as *Argyrosaurus superbis*?

Diagnosis. A huge-sized titanosaurid. Stout humerus with broad proximal end that has a straight upper edge (margin) perpendicular to the long axis of the bone. Pectoral muscle insertion area far more prominent and projected forward and medially. Ulna with extremely robust proximal end showing prominent edges delimiting markedly concave facets. Stout metacarpals approximately one-third the length of the humerus.

Description

At the time of Lydekker (1893) and Huene's (1929a) descriptions, the *Argyrosaurus* material was not adequately prepared. After the 1–2 cm thick coating of matrix was removed, it could be seen that the general morphological characteristics are much as they were described in those earlier papers.

The humerus (Pl. 66:1 and 3) is a long, straight bone with a thick deltopectoral crest bearing a strong prominence projecting anteriorly and medially for the insertion of the pectoral muscle. The medial edge shows an obvious anterior enlargement. The distal end is poorly preserved.

The ulna (Pl. 66:2 and 3) is well preserved with the exception of some damage to the proximal part. It is long, straight, and extremely stout at the proximal end as a consequence of the strong development of its three edges which delimit deeply concave facets. The olecranon is directed laterally and slightly posteriorly.

The radius (Pl. 66:3) is complete although distorted by flattening. This damage affects the antilunar face of the proximal half and the ulnar face of the distal half, resulting in the loss of useful information. Preparation has been insufficient to provide information concerning the carpal on the cubital side.

The metacarpals (Pl. 66:3 and 4) are fairly long and robust, with a vertical arrangement and a strong contact

between their proximal ends, and disposed as an arch. This position is obtained thanks to the wedge form of the proximal ends of the three medium metacarpals. In contrast, metacarpals I and V have their proximal ends compressed.

Comparisons

Argyrosaurus superbis is large. Only *Antarctosaurus giganteus* and *Alamosaurus sanjuanensis* among known titanosaurids are of comparable size. The differences with *A. wichmannianus* are restricted mainly to the morphology of the deltopectoral crest of the humerus and the robustness of the metacarpals which is less in *Antarctosaurus wichmannianus*. Unfortunately poor preservation of the anterior limb precludes detailed comparison.

Alamosaurus sanjuanensis is represented by a complete and articulated anterior limb along with other elements of the skeleton. This form has a humerus with a relatively narrower diaphysis than that in *Argyrosaurus*, and in addition, it has a more concave edge on the internal side of the bone. The metacarpals are proportionally shorter in the North American species. There are also certain similarities as far as general morphology and proportions of the humerus, ulna and radius; but despite this, *Argyrosaurus* is a larger form and its metacarpals are considerably more slender.

It shares with *Saltasaurus* the stout character of the humerus, although its gait and the robustness index of the ulna and radius are smaller.

Titanosaurids have other differences with *Argyrosaurus*, most apparent in the stoutness of all comparable bones. *Aeolosaurus rionegrinus* should be considered as an exception because its long bones are more robust and heavy, although not so large.

Comments

This species is based upon material which usually does not display important diagnostic characters. In spite of this, the fact that this material has been found articulated makes possible the assessment of other characters of diagnostic value such as relative proportions among its elements, permitting a more precise characterization of the taxon.

Argyrosaurus superbis?

Plates 67, 68 and 69

Antarctosaurus sp. Bonaparte and Gasparini 1979, p. 402

Locality. Right bank of Río Senguerr, in the area of the bend of this river, to the south-east of the southern most part of the Sierra San Bernardo in Chubut Province.

Stratigraphic position. Lower part of the Laguna Palacio Formation (Bonaparte & Gasparini 1978) Bajo Barreal Formation (Sciutto 1981).

<i>Argyrosaurus superbis</i> ? Lydekker 1893, PVL 4628 Dorsal and caudal vertebrae				
	5 th ? Dorsal	9 th ? Dorsal	10 th Dorsal	2 nd Caudal
Total height	60.5*	75.0*	77.0*	70.0
Minimum width	20.0	16.5	—	—
Height of the concave articular surface	27.5	28.0	30.5	28.5
Width of the concave articular surface	30.0**	32.0**	35.0**	33.0
Distance between pre- and postzygapophyses	27.5	23.0	—	±16.0
Distance between the facets of the prezygapophyses	12.0**	22.0**	—	12.0**
Distance between the facets of the postzygapophyses	±12.0**	—	12.0**	—
* Measurements taken from incomplete part.				
** Measures taken from the preserved half.				

Table 19

Age. Late Cretaceous, possibly Senonian.

Specimens. PVL 4628, three dorsal and three caudal vertebrae, left scapula, humerus, radius, right and left ulna, right pubis, incomplete right femur, incomplete left tibia and various fragments of ribs (all of these specimens belong to the same individual and were found disarticulated).

Description

Axial skeleton

Three dorsal vertebrae (Pl. 69:1, 2 and 3) have been recovered, the most anterior is possibly the fifth, while the other two belong to the most posterior in the series. All these vertebrae have bulky centra. This clearly distinguishes this genus from others of the family in which dorsal vertebrae are known. The 5th? dorsal vertebra (PVL 4628/1) has a massive centrum with a reduced pleurocoel located in a depression bordered dorsally by a crest. The neural arch is more or less short, has concave lateral walls, and the anterior face is deeply concave. The incompletely preserved parapophyses are located quite high on the arch, approximately at the same level as the prezygapophyses and somewhat below the postzygapophyses. The diapophysis and parapophysis are joined by a well developed horizontal lamina, such as in *Titanosaurus* from Brazil.

PVL 4628-2 is a posterior dorsal. The centrum is short and chubby, and expanded towards the ends. A reduced pleurocoel is located in a depression rather wider than in the previously described vertebra. The neural arch is deeply concave laterally with limited depressions forward and aft between the laminae. The major anterior depression is delimited anteriorly by an infrapara-physal lamina, dorsally by the horizontal lamina, and posteriorly by an oblique lamina which links the base of the neural arch with the infradiapophysal lamina. Within this depression there is another, smaller one, with two small lamina forming a 'V' that points downwards. The

parapophysis is located slightly ventral to the diapophysis but very near this latter structure.

The neural spine slopes posteriorly and projects over the diapophyses. It is reinforced by prespinal, supradiapophysal and suprapostzygapophysal laminae.

The last dorsal vertebra (PVL 4628-3; Pl. 69:1) has a short and large centrum expanding towards the ends. The pleurocoel is poorly developed. The neural arch is low with concave lateral walls reinforced by oblique laminae which extend from the posteroventral region dorsally to contact the parazygapophysal lamina.

The neuropophysis, diapophysis and prezygapophysis have not been preserved, except for the bases of these structures. The neural spine is vertically oriented and the anterior position inferred for the diapophysis suggests it was the most posterior dorsal vertebra. (Compare with the tenth dorsal vertebra of the *Titanosaurinae* indet. from Peirópolis, Brazil illustrated in Plate 15:5).

The postzygapophyses are held in their dorsal position by two very sturdy laminae and ventrally, by two postzygapophysal laminae. There are no remains of structures such as the hyposphene-hypantrum, so common in Jurassic sauropods as well as primitive titanosaurs (e.g. *Epachthosaurus*).

Of the two available caudal vertebrae, the anterior one (PVL 4628-4) deserves special attention owing to its preservation. The other one is represented by a first caudal vertebra that is so poorly preserved it is impossible to be sure whether or not it is biconvex.

PVL 4628-4 probably was the 2nd or 3rd caudal vertebra. It has a broad, procoelous and strikingly short centrum. The transverse processes are short, broad at the base and

<i>Argyrosaurus superbus?</i> Lydekker 1893	
Scapula	
Length	152.0
Maximum distal width	40.0
Minimum width	26.0

Table 20

<i>Argyrosaurus superbus?</i> Lydekker 1893	
Humerus	
Length	129.0
Maximum proximal width	43.0
Maximum distal width	45.0
Perimeter of the minimum section	62.0
Robustness ratio	0.48

Table 21

thinning dorsally, continuing as a vertical lamina that supports the prezygapophyses. The neural arch is very short, almost laminar and rather tall. The neural spine is tall, transversally expanded at its distal end, curved and concave in front. The neurapophysis is reinforced by prespinal and two supraprezygapophysial laminae. Probably it had others on the posterior face of the spine, but this region has not been preserved.

The humerus (4628-6) is a long bone, broad at the ends, and rather stout at the diaphysis. The proximal edge is quite straight and almost perpendicular to the lateral edge. The coracobrachial insertion is developed as a swelling. The deltopectoral crest is weakly developed, steepening towards its termination at the pectoral insertion. The

<i>Argyrosaurus superbus?</i> Lydekker 1893	
Ulna	
Length	83.0
Maximum proximal width a	
Maximum proximal width b	
Maximum proximal width c	
Maximum distal width	21.5
Perimeter of minimum section	41.5
Robustness ratio	0.50

Table 22

humeral head is not prominent, and there is a prominent area for a muscular insertion on the posterior face opposite the pectoral crest that is rugose and projects away from the body of the bone. The posterior distal

depression is wide and fringed by smooth lateral edges. This depressed area is one-third as long as the bone.

The ulna (PVL 4628-8) is a short bone, robust at its proximal end. This half is constituted by three thick lamina converging towards the bone axis, making a relatively light structure, considering the size and

<i>Argyrosaurus superbus?</i> Lydekker 1893	
Radius	
Length	70.0
Maximum proximal width	23.0
Maximum distal width	22.5
Perimeter of minimum section	41.5
Robustness ratio	0.58

Table 23

<i>Argyrosaurus superbus?</i> Lydekker 1893 PVL 4628	
Pubis	
Length	114.0
Maximum distal width	45.0
Minimum width	43.0
Iliac articulation width	35.0

Table 24

robustness of the proximal lamina. Only the articular and olecraneal regions are solid, while the proximal region is no thicker than 6–7 cm. The distal half is narrower, and has no laminae but instead a prismatic shaft of triangular section. The olecranon projects some 12 cm above the proximal articular surface.

The right pubis (Pls 68:1 and 70:4) is missing a small medial portion of the ischiadic articulation. The pubic lamina is broad with a straight distal edge perpendicular

<i>Argyrosaurus superbus?</i> Lydekker 1893 PVL 4628	
Femur	
Preserved length	117.0
Maximum proximal width	44.0
Perimeter of the minimum preserved section	81.0

Table 25

to the long axis of the lamina which shows a moderate thickening. The iliac process is broad and rather thick, while the articulation, although a very extended surface, is not very thick in the proximity of the acetabulum, which narrows towards the sagittal plane. The foramen is closed with a diameter of 13 cm wide x 4.5 cm high.

Only the proximal half of the right femur (PVL 4628-10; Pls 68 and 70: 5) has been preserved. It shows a bulky articular head with a remnant of the convex transverse facet preserved on its medial face. The proximal contour is not perpendicular to the long axis of the bone, but oblique and descending from the femoral head to the major trochanter, forming a highly obtuse angle with the lateral edge of the proximal half of the bone. The fourth trochanter is not prominent.

The distal part of the tibia (PVL 4628-11) and the distal two-thirds of the fibula (PVL 4628-12) are preserved. The fibula is straight and robust. Its outer face is markedly convex with a lateral tuberosity located dorsal to a less prominent elevation, as is the case in *Saltasaurus*, *Neuquensaurus* and *Titanosaurus*.

Almost the entire astragalus (PVL 4628-13) has been preserved, missing only part of the medial wall. In proximal and dorsal view there is a prominent and wide anteroposterior elevation which is part of the articular surface that contacts the fibular condyle of the tibia. The surface descends first anteriorly and then medially, this being the region that articulated with the medial condyle of the tibia. This elevation shows a rather vertical concave lateral face, this surface articulating with the fibula, and a vertical medial face which has a deep depression.

Comparisons

There is a strong resemblance between the holotype of *Argyrosaurus superbis* Lydekker 1893 and this material in the general morphology, humeral proportions, and particularly the ulna. Unfortunately, the only comparable material are those elements mentioned because the radius is ill-preserved and the metacarpals are absent on this specimen.

The dimensions of the bones of the forelimb and the morphology of the dorsal vertebrae differentiates it clearly from known saltasaurines and titanosaurines by the relative size of the very short vertebral bodies, the shallow convexity of the anterior articulation of the posterior dorsal vertebrae, and by their having a low and laterally cleaved neural arch (Pl. 73:1a, 2b and 3a). Bonaparte and Gasparini (1979) assigned this material to *Antarctosaurus* sp. owing to the partial resemblance of the fibular lateral tuberosity between the two forms. Nonetheless, the significant differences in the scapular morphology together with the impossibility of adequately comparing the remainder of the skeletons, favours the provisional dismissal of this interpretation.

Comments

This specimen is important, owing to the fact that it is composed of elements belonging to a single individual. Unfortunately the material on which the species *Argyrosaurus superbis* is based, although well preserved, only permits the tentative allocation of this material to that species. It is probable that future exploration in the area of Carlos Ameghino's site may one day allow a more precise determination.

cf. *Argyrosaurus*

Antarctosaurus wichmannianus? Huene 1929a, p. 75.

Argyrosaurus superbis Huene 1929a, p. 80.

Locality. Outcrops at Sierra de San Bernardo, 45 km to the west of Sarmiento locality, Chubut Province (Huene 1929a).

Stratigraphic position. Chubut Group, 'San Jorge Formation' according to the records of the Field Museum of Natural History. It is not possible to determine which formation within the Chubut Group was the source of these specimens.

Age. Late Cretaceous, probably Senonian.

Specimens. FMNH-P 13019 (= Px 13326) and FMNH-P 13018. Right femora. FMNH-FP 13020 (= 13436). Left tibia.

Description

The right femur (FMNH-P 13019=P13326; Pl. 70:2) is a complete, straight and robust bone. The massive articular head has a well marked convex medial facet oriented anteroposteriorly. It has three areas of muscular attachment in the area of the 4th trochanter: one well marked on the trochanter for the *caudofemoralis longus m.* and the other situated anteriorly for the *puboischiofemoralis internus*. The third on the posterior face was for the *caudofemoralis brevis*. On the distal end there is a well developed condyle, directed backwards. The condyles are the limits of the depressions of which the anterior is barely visible, while the posterior is deep. Its robustness index is 0.494.

This specimen was assigned by Huene (1929a) to *A. wichmannianus*. Another right femur (FMNH-P 13018; Pl. 70:1) is rather longer, and assigned by Huene (1929a; p. 80–81, Pl. 38:3) to *Argyrosaurus superbis*. It shows slight differences in the proximal outline, the region of the major trochanter being less striking. In any case, this area is not well preserved. In the area of the fourth trochanter there are minor differences compared to the previously described femur, showing more pronounced and extensive rugosities, except for the insertion area of *caudofemoralis longus*, which is not very prominent.

A complete left tibia (FMNH-P 13020; Pl. 70:3), massive at its ends, bears muscular insertion rugosities that are particularly marked on the anterior side of the cnemial crest and on the distal third of the anterior medial edge.

Comments

In the present revision the material has been assigned to cf. *Argyrosaurus* sp. on account of similarities with the femur and tibia of *Argyrosaurus superbis* documented from the same region and probably from close to or even the same stratigraphic position. Huene (1929a) referred part of this material to *Antarctosaurus wichmannianus*, a species documented in the Neuquina basin. As determined in the present work, the femur and tibia lack clear diagnostic features, except in the case of the robustness and proportions of some material.

Genus *Epachthosaurus* Powell 1990

Type species. Late Cretaceous, possibly Senonian.
Diagnosis. The same as for the type species.

Epachthosaurus sciuttoi Powell 1990.
Plates 71 and 60

Holotype. MACN not numbered (Pls 66:5, 71). Some incomplete posterior dorsal vertebrae.
Paraplasto type. MACN Not numbered. Six posterior incomplete articulated dorsal vertebrae articulated with the also incomplete sacrum and a fragment of the pubic peduncle of the ilium. This plaster cast was obtained from a mould at the site, because it was technically impossible to extract the bones at that time, Dr JF Bonaparte (pers. comm.).
Referred material. An articulated skeleton lacking the skull, cervical and anterior dorsal vertebrae housed at Universidad de La Patagonia ‘S. J. Bosco’ (Powell 1986; Martínez et al. 1991).
Diagnosis. Centra of the dorsal vertebrae relatively large, very broad and depressed. Pleurocoels very large and deep as in the other known titanosaurs. Neural spines of the posterior dorsals anteroposteriorly compressed, with prespinal laminae thickened and well developed, forked at the lower part, forming the spinal-prezygapophyseal lamina. Accessory articulations are present but distinct from the hypsophene-hypantrum structures. The diapophysis without a flat surface at the dorsal end.

Description

The holotype is a vertebra with a relatively short and very thick centrum, and a large and deep pleurocoel.

The neural arch is short, with a neural canal well developed especially in the dorso-ventral diameter. The diapophyses project at a 45° angle to the sagittal plane, and do not have the dorsal flattening on the distal end as seen in *Saltasaurus* and other genera of the family Titanosauridae.

The parapophyses have not been preserved and appear to have been located high on the arch as no vestiges are seen of them on the centrum nor on the lateral wall of the neural arch, so this is assumed to be a medial or posterior dorsal vertebra. The limited length of the centrum, and the vertical disposition of the supporting structure for the neural arch corroborates the likely identification of this vertebra as a posterior dorsal.

The neural spine was not preserved, but the basal part indicates a pre-spinal lamina which is highly developed and is characterised by a peculiar forking at the base, to form the lamina of the spinal-prezygapophysial walls. These laminae bound a deep depression that opens laterally. A horizontal lamina is situated above the neural canal.

The plastotype MACN is made up of a series of posterior dorsal vertebrae and a large part of the articulated sacrum, which complements the information provided by the holotype of this new form.

The better preserved dorsal vertebrae correspond to the eighth, ninth and tenth of the series.

The centra diminish in length between the sixth and the tenth of the series. These are low, very broad and gently convex, in the transverse sense, on the ventral surface. The pleurocoels are large and deep, forming the ‘eye’ marking the definite edge.

<i>Epachthosaurus sciuttoi</i> Powell 1990								
Posterior dorsal vertebra (Holotype)								
Total length	23.5							
Length without anterior articular condyle	11.0							
Total height	31.0*							
Minimum width of the centrum	13.5							
Height of posterior articular surface	13.0							
Width of the posterior articular surface	15.5							
Paraplastotype's measurements								
	6 th dorsal	7 th dorsal	8 th dorsal	9 th dorsal	10 th dorsal	1 st sacral	2 nd sacral	3 rd sacral
Approximate length without the articular condyle	24.5	24.5	24.0	18.5	16.0	13.0	15.5	15.5
Minimum width of the centrum	21.0	21.0	21.5	24.5	24.0	14.0	13.0	16.0
* Measurements on preserved portion								

Table 26

The neural arch shows depressions which are generally triangular and bounded by laminae that are much shorter on the tenth dorsal vertebra.

The neural spines are very compressed anteroposteriorly. In the ninth there can be seen a notable development of the prespinal lamina, which is bifurcated below into two laminae which are joined to the prezygapophysis: this also occurs in the holotype.

Bonaparte (pers. comm.) has observed during work in the field, that these dorsal vertebrae are characterised by a distinct accessory articulation known as hyposphenohypantrum, found in the sauropods of the Jurassic. The same investigator has pointed out the presence of ossified ligaments on the neural spines of the sacral vertebrae and the posterior dorsal vertebrae. Unfortunately, these peculiar structures documented for the first time among the titanosaurids, are not preserved in the holotype nor is there any clear evidence in the paratype.

There are five centra in the preserved sacrum of the paraplotype. In ventral view can be seen some sacral ribs and part of the pubic pedicle of the right ilium. The centra of the sacral vertebrae are relatively large, only seen to the limit as one side differing in these details from the advanced ossification seen in *Saltasaurus loricatus*.

The ventral face of the centra of the 3rd, 4th and 5th sacral vertebrae show medial depressions.

Details of the characters of the articulated specimen mentioned by Powell (1986) and Martínez et al. (1991) are considered by Sanz et al. (1991) and in the phylogenetic appendix included in the present contribution.

Comparisons

The dorsal vertebrae of *Epachthosaurus sciuttoi* have peculiar characteristics clearly quite different from the other forms described here of the Family Titanosauridae in which the dorsal vertebrae are known.

The differences consist in having a thick, broad centrum with a flat ventral surface, a great development of the pleurocoels in size and depth, and finally the plate-like accessory articulation which does not correspond to the hyposphenohypantrum, as was pointed out above.

It is unique also in having a ventral pre-spinal bifurcated lamina that is united to the prezygapophyses. One lamina forms a division of the pre-spinal lamina, which is also seen in some of the vertebrae of the articulated dorsal series from Pterópolis, referred here to subfamily Titanosaurinae. These, nevertheless, are much weaker and do not have a division of the pre-spinal lamina, but an additional reinforcement which attaches to the diapophyses.

The dorsal vertebrae of *Argyrosaurus superbus* from the bend of the Río Senguerr, which also have a large

centrum, differ in that the pleurocoels are reduced; they are placed higher and lack the ventral planation characteristic of *Epachthosaurus*.

Comments

Unfortunately technical problems have impeded the extraction of the specimens which constitute the paratype. It is for this reason that a cast of plaster was used here as the plaster paratype, with the object of complementing the information provided by the holotype.

Although it is not possible to see with clarity the additional articulations mentioned by Dr JF Bonaparte (verbal communication), it is the case that these casts faithfully produced many anatomical details. The morphological characteristics of this species are characters unique to the family Titanosauridae. The remarkable accessory intervertebral articulations have evolved as an adaptation which restricts the possibility of a rotation of the vertebrae.

Genus *Pellegrinisaurus* Salgado 1996

Type species *Pellegrinisaurus powelli* Salgado 1996.

Distribution. Late Cretaceous, Campanian-Maastrichtian.

Diagnosis. The same as for the type species.

Pellegrinisaurus powelli Salgado 1996 Plate 72

Pellegrinisaurus powelli Salgado 1996; pp. 355–65,
cf. *Epachthosaurus* sp. Powell 1986 pp. 324–28

Holotype. MPCA 1500. Four dorsal vertebral centra, 26 incomplete caudals and an incomplete right femur.

Locality. South margin of Lago Pellegrini, known as quarry of the 'Pala Mecánica' in General Roca Department, Río Negro Province.

Stratigraphic position. Lower member of the Allen Formation (Malargue Group).

Age. Late Cretaceous, Early Maastrichtian.

Diagnosis. Large titanosaurid characterised by strongly depressed dorsal centra, midposterior and posterior caudals with anteroposteriorly elongated and dorsoventrally depressed neural spines, the anterior ends of which are higher than the posterior ones. Transverse width of the centrum of the posterior dorsals approximately twice the maximum dorsoventral depth.

Description

Only some of the dorsal vertebral centra are preserved. They are very wide, depressed and low, having large pleurocoels. The vertebra MPCA 1500-1 is similar to an anterior dorsal, outstanding in its length, having a large and deep pleurocoel, of such a shape that it is separated from the corresponding depression of the pleurocoel of the opposite side by a partition approximately 2–5 cm thick. The ventral face is very broad, almost flat in MPCA 1500-4.

The remainder of the dorsals (MPCA 1500-3/4/5) are poorly preserved, but it is easy to see that they also possess a well developed pleurocoel. The length of the centrum is appreciably diminished.

Unfortunately, problems relating to the work of excavation, and preparation, have caused the deterioration of a large part of the vertebral column, which were originally very complete in the dorsal, caudal and sacral region (Pl. 72).

Actually, some dorsal centra were preserved, as well as a fragment of the sacrum and a large part of the caudal vertebral series. Among these last are some almost complete specimens.

Professor Roberto Abel, Director of the Museo Provincial 'Carlos Ameghino' of Cipolletti generously made available photographs taken at the time of the excavation. In these, it can be seen that originally all of the dorsal vertebrae were present and articulated. In these photos, most are complete specimens with depressed centra, large pleurocoels, low neural arches and a prominent development of the reinforcing laminae of the prezygapophysis that was linked to the lateral part of the neural arch by a well developed infra-diapophysial lamina.

The sacrum is very incompletely preserved: present are the 5th, 6th and part of the 4th sacrals.

Of the caudal vertebrae, a series of 27 specimens were preserved in succession almost without interruption. Of the first caudal (MPCA 1500-7), only an incomplete centrum is preserved. It is biconvex and shows the base of a transverse lateral laminar process, the major axis of the cross section of which is vertical. Below the base of the transverse lateral laminar process is located a pleurocoel, which is also seen on other vertebrae following in the sequence (MPCA 1500-8/9).

The vertebra MPCA 1500-12 (10th?), is one of those which have been completely preserved and approximately corresponds to the tenth caudal. It is characterised by having a centrum which is more broad than high, resembling in this aspect the Saltasaurine, but having a vertical and laterally compressed neural spine. The prezygapophyses are long, as in the Titanosaurinae. The ventral face of the centrum is broad and somewhat transversely convex, without the accentuated depressions which are seen in the Saltasaurines.

Specimen MPCA 1500-13 consists of two articulated vertebrae, of which the anterior one is almost completely preserved and has similar characteristics to the one described above (MPCA 1500-12), although here the neural spine is inclined backward at 45° and the transverse process is horizontal and rudimentary.

The posterior vertebrae are long and somewhat depressed. In the anterior view, the centrum of MPCA 1500-27 (approximately the 24th caudal) is also very long and depressed, with no neural spine.

Comparisons

The dorsal vertebrae, interpreted from the preserved specimens and photographs obtained during the excavation, show that they are similar to *Epaclithosaurus sciuttoi* in the broad centra, the low neural arches and the development of the reinforcing lamina of the apophysis and pleurocoels.

With respect to the caudal vertebrae, it is seen that some characters (morphology of the centra) are similar to that of the Saltasaurinae, although others (the neural spine laterally compressed and positioned vertically, and the possession of long prezygapophyses) occur in the Titanosaurinae.

Comments

The strong anatomical similarities of the vertebrae of these specimens from Lago Pellegrini to those of *Epaclithosaurus sciuttoi*, coupled with the fact that this type of morphology is not seen in any of the other taxa of the family where the dorsal vertebrae are known, is the basis for identifying them here as cf. *Epaclithosaurus* sp. until additional material is found.

Salgado (1996) redescribed this material and referred it to a new genus and species: *Pellegrinisaurus powelli*.

Genus *Clasmodosaurus* Ameghino 1898
Nomen dubium

Clasmodosaurus Ameghino 1898, 1921, p. 703;
Huene 1929a, p. 140; Bonaparte 1978, p. 552.

Type species. *Clasmodosaurus spatula* Ameghino 1898.
Distribution. Late Cretaceous of Santa Cruz Province.

Clasmodosaurus spatula Ameghino 1898

Clasmodosaurus spatula Ameghino 1898, 1921;
Huene 1929a, p. 140, (Not given). Pl. 40:3-5;
Bonaparte 1978, p. 552

Holotype. Personal collection of Ameghino. Without a number.

Locality. Río Schuen, Santa Cruz Province.

Age. Late Cretaceous.

Specimens. Three incomplete teeth.

Description

According to Huene (1929a), these teeth are of the cylindrical type, slightly labiolingually compressed (labiolingualmente) with the apical 3/4 covered with enamel, where slight longitudinal grooves can be seen.

The root is quite distinct from the crown. Huene (1929a; Pl. 40:3–5) shows that the preserved apical ends are conical, laterally compressed, and with both edges limiting the labial as well as the lingual faces.

Comparisons

These teeth are of the diplodociform pattern, comparable to those known in *Diplodocus*, *Antarctosaurus*, *Alamosaurus sanjuanensis* (Kues et al. 1980) and undetermined titanosaurids (in this paper). It differs from those by the longitudinal grooves present in both lingual and labial faces.

Comments

I accept Ameghino's original interpretation of these teeth as sauropod as correct. Because of the geographic and stratigraphic context, they can be included in the titanosaurid family.

Huene (1929a), after a rather confused analysis of this form, seems to consider it as a theropod, and as a sauropod as well. In his comparison he only considered the longitudinal crests to be of diagnostic value, comparing them to those of *Labrosaurus*, and even considering the possibility that they might belong to *Loncosaurus argentinus*.

Bonaparte (1978) agrees with Huene (1929a, in part) referring to this material as a theropod.

Dinosaur dental morphology by itself can't be considered as a reliable diagnostic character. On this basis *Clasmodosaurus spatula* is considered as *nomen dubium*.

Genus *Campylodoniscus* Kuhn 1970 *Nomen dubium*

Campylodon Huene 1929a, pp. 82–3, *non*; Cuvier and Valenciennes, 1832 in Steel 1970; White 1973, p. 125; Bonaparte 1978, p. 562; Bonaparte and Gasparini 1979. *Campylodoniscus* Kuhn 1961 in Steel 1970) p. 76; White 1973, p. 125; Olshevsky 1978, p. 27.

Type species. *Campylodon ameghinoi*; Huene 1929a.

Distribution. Late Cretaceous, possibly Senonian of the Sierra de San Bernardo, Chubut, Argentina.

Diagnosis. The same as for the type species.

Campylodoniscus ameghinoi (Huene 1929a), Kuhn 1961
Nomen dubium

Campylodon ameghinoi Huene 1929a, pp. 82–83, Pl. 40:1–2; Bonaparte 1978, p. 562; Bonaparte and Gasparini 1979, p. 402.
Campylodoniscus ameghinoi Kuhn, in Steel 1970, p. 76.

Holotype. MACN A-IOR63. An incomplete left maxillary with seven alveoli, one functional tooth, and another isolated broken replacement crown.

Locality. Not precise. Western flank (Huene 1929a) of the Sierra de San Bernardo, to the west of Lake Musters.

Stratigraphic position. Chubut Group. There is no existing data permitting knowledge of the formation which provided this specimen.

Age. Late Cretaceous possibly Senonian.

Specimens. Only the holotype.

Description

It is a relatively short and tall maxillary, reminiscent of *Camarasaurus* Cope, (Gilmore 1925). The lower edges and the posterodorsal area are incomplete. It has a total of seven alveoli with a tooth erupting in the 5th. Moreover, a partially erupted replacement tooth can be seen in the same alveolus.

The external face is perforated by various foramina. The largest of these is located above the first alveolus. Posteriorly, they diminish in size.

The internal face exhibits anteriorly a medial projection which extends the surface of contact with the premaxillary; there is evidence of a crenulated articulation. Behind the projection is seen a longitudinal elevation which extends to the extreme posterior end of the bone.

The teeth are cylindrical, with the distal part or apex spatulate. The surface of the enamel is rugose, a character determined by longitudinal striations, which are irregular and discontinuous. On the root of the tooth, the surface is smooth.

As in *Camarasaurus*, *Brachiosaurus* and the cetiosaurs, the edge of the tooth is curved backward and shows a certain bulbous nature above the labial face, to the height of the inflection of the axis.

Although in general the labial face is strongly convex, it is slightly concave adjacent to the lateral edges, as in *Camarasaurus*.

The lingual face has, transversely, a convexity less accentuated than the external one, and a smooth medial longitudinal elevation can be seen.

Comparisons

Unfortunately there is no knowledge of other maxillaries among the titanosaurids. Detailed examination of the dental morphology of *Campylodoniscus ameghinoi* indicates that there is a clear structural similarity between its tooth and the type of *Camarasaurus* in having a clear differentiation between the crown and the root by the presence of enamel, the possession of a backwards curved edge, the bulbous nature of the labial face and the transverse surface concavity which is parallel to the anterior and posterior edges of the tooth.

The known teeth of the titanosaurs (*Antarctosaurus*, Huene 1929a, *Alamosaurus*, Kues et al. 1981), of the Titanosaurinae indet. (Powell 1979 and this work), as well as the abundant collection from Maastrichtian deposits show that they have a straight edge, and are approximately symmetrical, the enamel face is smooth or slightly rugose (in this last case, the striations are long, approximately straight and continuous) and do not have the bulbous expansion on the lateral face.

The fact is that the teeth of *Campylodoniscus* are not very wide relative to the height of the labial bulbous expansion giving it a superficial intermediate aspect between the teeth of the Diplodociformes and the Camarasauriformes as pointed out by Huene (1929a) and Bonaparte (1978).

Comments

This specimen was originally described by Huene (1929a) as *Campylodon ameghinoi*, but this name had been previously used by Dumeril in 1853, and Cuvier and Valenciennes (1832)—Kuhn 1961 in Steel (1970) for which Kuhn (op. cit.) proposed the substitute generic name *Campylodoniscus*.

Campylodoniscus ameghinoi was studied by earlier authors such as Huene (1929a). Owing to the incompleteness and fragmentary nature of the specimen plus the fact that 'diagnostic characters of all the sauropods of Patagonia are all based on the morphology of the postcranial skeleton', Bonaparte and Gasparini (1979) considered this taxon to be a *nomen vanum*. The argument of Bonaparte and Gasparini (1979) is tenable in part. Likewise, the new evaluation of the characters given in this work indicates the importance of cranial remains for the diagnosis of the different genera (e.g. *Antarctosaurus* and *Saltasaurus*). It is certainly true that until recently there was no knowledge of the maxillaries in any of the formally documented genera in South America, aside from those pertaining to *Antarctosaurus*, and this form has relatively small teeth in the adults. Neither can be assigned to either *Saltasaurus* or *Neuquensaurus* because they are not large enough nor have they been recorded from the Late Cretaceous in that region.

Of the two known genera, remains of *Titanosaurus* have not been documented in this area but *Argyrosaurus* is known on the basis of various specimens of the postcranial skeleton. There exists then the very real possibility that it corresponds to the last genus or some distinct form. At present it is therefore convenient to consider *Campylodoniscus ameghinoi* as a *nomen dubium*, according to the definition in the Code of Zoological Nomenclature.

This specimen has a 'camarasauroid' as opposed to a 'diplodocoid' morphology (in an adaptive sense which seems to be present also in *Antarctosaurus wichmannianus* and which has been inferred to be typical of the family Titanosauridae).

It is worthwhile to record here that Huene and Matley (1933) described a short, tall maxillary which occurred along with *Antarctosaurus* in the 'strata with carnosaurus' at Bara Simla, Jabalpur, India.

On the other hand, another cranium found at Arroyo Morterito, Department of Candelaria, Salta Province must be considered. It is a short and tall premaxillary which cannot possibly be regarded as a 'diplodocoid' cranium.

This evidence strongly indicates the possibility that, among the forms now considered to belong to the Titanosauridae there exist two groups with markedly different cranial structure.

Titanosaurinae indet.
Plates 13–15

Locality. Peirópolis, close to Uberaba, State of Minas Gerais, Brazil.

Stratigraphic position. Lower and middle part of the Baurú Formation.

Age. Late Cretaceous, Senonian.

Material. DGM. 'Series A'(?). Complete series of cervical vertebrae, except the atlas, including the axis, 11 cervical vertebrae, and three anterior dorsals (Pls 13,14:1-4,14:6-8). DGM 'Series B'(?). Five cervical vertebrae, 10 dorsals (the last cervical and all of the dorsals are articulated), a sacrum with the ilium articulated, and 10 partially articulated caudal vertebrae (Pls 14:5,15).

Description

DGM. 'Series A' (Pls 13 and 14)

Cervical vertebrae

Besides the axis, there are 11 cervical vertebrae that represent the complete cervical series and were found articulated. The axis has a relatively tall centrum compared to *Saltasaurus loricatus* and the neural spine is inclined backwards. The vertebrae are characterised by being long, tall and relatively low. The axial centrum is tall and slender. The ventral face is concave forward, and somewhat convex on the posterior third. The lateral walls have a broad depression where there usually is a small pleurocoel. The base of the parapophysis is laminar, and attaches to the centrum along a plane parallel to its axis. It differs in this aspect from the vertebrae of *Saltasaurus* and *Neuquensaurus*.

The diapophyses are practically laminar on the distal part of the anterior cervicals, and form a ridge parallel to the axis of the vertebrae, becoming more convex in the posterior cervicals, particularly in the 8th. Prezygapophyses and postzygapophyses are relatively short, and project slightly (both anteriorly and posteriorly), in relation to the centrum's ends. The neural spine is very low and inclined posteriorly, back to the 6th cervical. At the 7th, the neural spine is divided and becomes much higher and thicker. All of the cervical vertebrae have prespinal and postspinal fossae. These are located behind the spine and between the

Titanosaurinae indet. 'Series A' of Peirópolis, Brazil											
Cervical Vertebra	3 rd	4 th	5 th	6 th	7 th	8 th	9 th	10 th	11 th	12 th	
Total length	19.5	20.8	21.0	25.5	23.5	24.5	—	23.0	21.0	—	
Length without posterior articular condyle	18.0	18.9	21.5	23.5	20.5	21.0	—	20.0	17.0	10.3	
Total height	—	4.7	11.3	11.7	14.5	13.5	—	19.0	—	17.0	
Minimum width of ventral face of the centra	—	3.1	3.6	3.9	4.4	—	—	—	10.9	8.8	
Height of the posterior articular surface	2.9	3.6	4.2	3.9	3.7	2.6	—	6.5	8.0	—	
Width of the posterior articular surface	3.8	4.7	5.0	5.7	5.8	7.0	—	8.9	12.8	—	
Distance between prezygapophyses articular facets.	—	6.4	6.8	7.0	8.1	7.7	—	—	12.2	—	
Distance between postzygapophyses articular facets	—	6.8	7.1	6.2*	6.8*	7.6	—	—	—	—	
Distance between pre- and postzygapophyses	—	18.0	21.2	23.5	22.5	23.0	—	23.0	—	—	
* Measurements taken from incomplete part.											

Table 27

Titanosaurinae indet. 'Series A' of Peirópolis, Brazil			
Dorsal Vertebra	1 st	2 nd	3 rd
Total length	15.0	14.0	14.0
Length without anterior articular condyle	11.5	10.0	12.0
Total height	24.2	25.5	25.0
Minimum width of the centrum	13.7	13.5	14.0
Height of posterior articular surface	8.2	8.0	8.6
Width of the posterior articular surface	13.5	11.6	11.0
Distance between the centrum and prezygapophysial facets	15.5	14.0	11.4
Distance between the centrum and postzygapophysial facets	13.6	11.0*	12.0
Distance between pre- and postzygapophyses	12.0	8.4	11.5
* Measurements taken from the preserved half.			

Table 28

postzygapophyses and are always deep. Several vertebrae of the series have been preserved with part of the ribs in articulation. The 8th cervical is completely preserved (Pls 13:8, 14:3). The cervical ribs of the latter are long and slender. They extend more or less parallel to the centrum's axis. The anterior projections are incomplete and extend beyond the anterior end of the centrum. The posterior projection extends for less than 11 cm behind the posterior edge of the centrum. There is part of an incompletely preserved 9th or 10th cervical vertebra. The length of the centrum of this vertebra is appreciably diminished, in accordance with the abrupt passage to the dorsals.

Dorsal vertebrae

The cervical-dorsal transition is visible. The first three dorsals of 'Series A' are preserved. The first dorsal centrum is very short in contrast to the last cervicals,

whose centra are much longer. The pleurocoel is reduced and located immediately behind the parapophysis. The neural arch is tall and wide. The diapophyses are thick, broad and project laterally and forward. These structures are supported by the infra-diapophysial lamina which inclines forward. The articular facets of the diapophyses are oriented laterally and downward. The facets of the pre- and postzygapophyses are supported by thick columns formed by the widening of the infra-prezygapophysis and supra-postzygapophysis. Relatively short neurapophysis characterise the dorsal vertebrae. It is reinforced by the axial pre- and postspinal laminae, as well as by the longitudinal elevations or columns which form at the expense of the spinal-prezygapophysial and supradiapophysial laminae. The centrum of the second dorsal is much shorter and smaller than that of the first dorsal, showing a smaller pleurocoel. The neural arch is very short and broad.

The 3rd dorsal is quite different to 1st and 2nd elements. The centrum is short and thick, but has a much more developed pleurocoel. The neural arch is short and broad, joining the parapophysis upon its lateral face. The diapophyses are located approximately at the middle of the centrum, projecting laterally and upward. The supporting infradiapophysial laminae form an almost vertical plane. The neural spine is somewhat inclined backwards and is situated at the very end of the centrum. It is reinforced by prespinal and postspinal laminae, or supradiapophysial ridges. Here there are not the spinal-prezygapophysial laminae which are seen on the first and second dorsals. The pre- and postzygapophysial facets are appreciably reduced.

DGM ‘Series B’ (Pls 14 and 15)

Cervical vertebrae

The cervical vertebrae are, generally, much larger than those of ‘Series A’ and some of these are much shorter and robust.

The last cervical is well preserved. The centrum is relatively depressed, with the transversal diameter greater than the dorsoventral one. The neural arch is higher and laterally expanded. The diapophyses are large and have facets oriented backward and downward. The prezygapophyses and postzygapophyses are short and have large articular facets. The neural spine is short and is strengthened by large lamina or pillars: a prezygapophysial, a supra-diapophysial and a thick supra-postzygapophysial laminae.

Dorsal vertebrae

The first dorsal has a much shorter centrum than the last cervical. The pleurocoel is more reduced, with sharp edges. The ventral face of the centrum is convex owing to the upward ‘drift’ of the parapophysis. The neural spine is incomplete, but there is enough preserved to deduce that it was low and undivided, closely linked to the

postzygapophysis and reinforced anteriorly by an enlarged column as in ‘Series A’. This vertebra is somewhat different from the first dorsal of ‘DGM. Series A’, as they have spinal columns without prominences and in the possession of these characteristics they are typically more prominent in the dorsal vertebrae.

The 2nd dorsal has a more reduced pleurocoel than the first, with the parapophysis situated higher on the centrum. The diapophyses are large and somewhat inclined forward, the same as the supporting laminae. The neurapophysis inclines a little bit backward and has the postzygapophyses strongly attached. The distance between the facets of prezygapophysis and postzygapophysis is smaller than in the dorsal and cervical series, a pattern which corresponds to the point of maximum dorsally concave flexure of the cervical-dorsal section of the vertebral column. The differences between these vertebrae and their equivalents in the DGM ‘Series A’, include the distance between the prezygapophyses and postzygapophyses which is less in the latter, and the possession of a thicker neural spine. The 3rd dorsal has a taller and shorter centrum. The parapophyses are close and located higher above the lateral face of the neural arch and it has some depressions. The neural spine is taller and is inclined 45° backward, differing distinctly from that of the first and second dorsals. This vertebra shows several differences in relation to those described above: the depression located between the prezygapophysis and the diapophysis is more developed. The former is seen to extend much further forward. The shafts of the diapophyses are notably broader in the dorsal view.

The centrum of the 4th dorsal is much higher and the pleurocoel is also elongated. The basal part of the neural arch is more anteroposteriorly extended and relatively low. The parapophyses are large and situated immediately under the prezygapophyses. The neural spine is tall and

Titanosaurinae indet. ‘Series B’ of Peirópolis, Brazil					
Cervical Vertebra	posterior indet.	posterior indet.	9th	10th	11th
Total length	27.0	27.5	7.0	5.0	20.0
Length without posterior articular condyle	24.0	25.0	23.0	20.0	16.0
Total height	—	18.4	16.0*	19.0*	16.5*
Minimum width of the centra.	6.0	5.4	6.8	8.0**	9.8
Height of posterior articular surface	9.5	8.5	10.5	13.0	—
Width of the posterior articular surface	5.1	5.0	6.2	6.0	—
Distance between prezygapophysial articular facets	12.0**	8.6**	12.0	12.2	12.5
Distance between postzygapophysial articular facets	11.7	9.5	13.5	13.0	10.4
Distance between pre- and postzygapophyses.	25.5	27.0	24.0	22.5	17.5
* Measurements taken from incomplete part.					
** Measurements taken from the preserved half.					

Table 29

Titanosaurinae indet. 'Series B' of Peirópolis, Brazil									
Dorsal Vertebra	1 st	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th	9 th
Length	—	13.0	—	15.5	—	—	—	—	15.8
Length without anterior articular condyle	10.0	9.5	9.5	12.0	12.5	13.5	13.5	13.3	12.0
Total height	17.0	—	23.0	—	12.5	—	—	16.0	—
Minimum width	8.0	7.7	—	7.3	6.4	6.2	7.5	7.2	8.4
Height of posterior articular surface	—	—	—	10.2	—	—	—	—	11.7
Width of the posterior articular surface	—	—	—	7.5	—	—	—	—	8.5
Distance between the prezygapophysial facets	12.0	±11.5	11.0	17.2	—	15.0	±12.0	±11.0	10.0
Distance between the postzygapophysial facets	10.0	9.5	8.8	±8.6	±7.7	6.3	6.3	5.0	—
Distance between pre- and postzygapophyses	11.5	10.0	12.0	12.5	13.0	14.0	14.5	—	±11.5

Table 30

straight, inclining 45° with respect to the axis of the centrum. It is laterally compressed, and is not as stout distally as in *Saltasaurus loricatus*. The prespinal lamina is well developed.

The 5th dorsal vertebra is very similar to the 4th, differing mostly in the higher position of the parapophyses and a greater distance between the parapophyses and the diapophyses which is interpreted as a part of the anterior infra-diapophysial depression.

The neural spine is anteriorly reinforced by a large development of the prespinal lamina and an accessory spinodiapophysial lamina which unites the diapophysis with the pre-spinal lamina.

The 6th, 7th and 8th dorsals appear to be alike. The first two have relatively tall and slender centra. The 8th is somewhat shorter. The pleurocoel is also elongated, clearly differing from *Saltasaurus*, *Neuquensaurus* and *Argyrosaurus* which have short centra, as is the case in the last species. The basal parts of the neural arches are relatively tall and are somewhat inclined anteriorly. The parapophyses and the diapophyses reach the same height. The former are located at the same level as the prezygapophyses. The diapophyses are broad in the dorsal view and have a plane surface on the upper part of the distal end. These structures are reinforced by thick laminae forming columns above and below. The anterior infradiapophysial fossa is large and deep. It is located below the horizontal lamina, between the parapophyses in front and the diapophyses behind. There is no indication of a developed posterior horizontal lamina, as is characteristic in *Saltasaurus loricatus*, firmly joining the postzygapophysis to the diapophysis. There is just an incipient lamina in that place. The neurapophysis is laterally compressed and does not have an enlarged distal end. It is greatly inclined backwards as are the former ones, but is much strengthened. The pre-spinal lamina is highly developed especially at the distal end. The

accessory supra-diapophysial lamina persists in the case of the sixth and seventh, but is not seen in the eighth. The supra-diapophysial lamina presents peculiar architecture; it forks upwards in two laminae in a 'V' attached to the base of the neurapophysis. This pattern is not seen in the eighth dorsal. The post-spinal lamina is equally developed. In the eighth, this structure is slightly divided in front to reach the level of the facets of the postzygapophyses, connecting the medial part of both.

The ninth dorsal has a centrum and a neural arch very similar to the eighth. The observed differences are the relative positions of the parapophysis and the diapophysis. They are joined very closely and a little in front, and somewhat below the second. The tenth dorsal has an appreciably shorter centrum, and a neural spine which is very compressed like the ninth, it is vertical and has an enlarged distal end as in *Saltasaurus loricatus*. The diapophyses and the infra-diapophysial lamina which supports it are inclined forward. The incipient horizontal posterior lamina, which is barely suggested in other vertebrae, is here well developed. The anterior infra-diapophysial depression is notably reduced in relation to the rest of the dorsals.

Pelvis

The size of the sacral vertebrae and their anatomical features suggest that this sacrum with an articulated ilium belongs to the Series 'B' of Peirópolis. This pelvis is exposed on the dorsal side and is lacking the right ilium and the upper part of the sacral rib on this side. The sacrum has six vertebrae. The last articulation is convex as in *Saltasaurus*. The first element, originally a dorsal, is incorporated to the sacrum. It has a short rib, articulated in the way of the dorsals, which goes over the upper edge of the preacetabular portion of the iliac lamina. All of the sacral vertebrae except the last two have the upper part of the end of the diapophysis, which also occurs in the last dorsals. The distance of these facets from the axial plane is smallest in the first and last sacral, both increasing,

until they reach their maximum distance at the middle of the sacrum and the height of the 3rd and 4th sacral vertebrae, where this structure is manifest over the transverse process.

The last sacral is a caudal incorporated into the sacrum. It has long processes which are connected with the ilium at its extreme distal extension, resembling in this aspect the first caudal vertebra of *Saltasaurus loricatus*. The neural spines are stout and rounded at the end, a swelling that is progressively reduced until the 3rd sacral. These reinforce the prespinal and postspinal laminae, which in some vertebrae fuse with the diapophysial or supradiapophysial laminae, and therefore with the diapo-prezygapophysial and diapo-postzygapophysial laminae. In lateral view, the neurapophysis projects above the dorsal margin of the ilium.

Caudal vertebrae

The centra are high and especially narrow below. The posterior articular surface is nearly vertical or very slightly inclined forward: it is slender and laterally compressed. The neural arches are inclined forward. The articular facets of the prezygapophyses are strongly inclined. Its planes form a very sharp angle with respect to the sagittal plane. The prezygapophyses are quite extended forward, but not as much as in *Aeolosaurus rionegrinus*. In contrast to that species, the postzygapophyses are located more to the rear, approximately at middle of the centrum. The neural spine has a well developed pre-spinal lamina above and two spinoprezygapophysial laminae at the base. Behind these is a post-spinal medial laminae and supra-postzygapophysial laminae.

Titanosaurinae? indet.
Plate 16:1a, 1b

Locality. Peirópolis, near Uberaba (identified as ‘Peirópolis 2’), Minas Gerais State, Brazil.
Stratigraphic position. Lower part of the Baurú Formation (Baurú Member or Facies).
Age. Late Cretaceous, Senonian (Huene 1939 in De Oliveira & Leonardos 1978).
Material. DGM s/number. A sacrum articulated to the right ilium and two dorsals.

Description

There is a pelvis with the sacrum with convex articular ends, with a fused right ilium. It is much larger than the other two sacral and the ilia discovered in Peirópolis. Moreover, two dorsal vertebrae are articulated to the sacrum.

Upon the neural spines of the 2nd, 3rd, 4th and part of the 5th sacral vertebrae, the belt of ossified ligaments were preserved, also found in *Epachthosaurus sciutoi*. The upper dorsal surface has a longitudinal ligamentary groove which indicates that the direction of distribution of the fibres are in two parts paralleling the axial plane, they diverge somewhat to the front. The presence of this ligament indicates that the posterior dorsal region and the sacrum have scant mobility in titanosaurids.

Comments

These specimens are comparable to those that are here identified with DGM-Series B of ‘Peirópolis 1’, and very probably correspond to the same genus and species. The only difference lies in their larger size. The most striking characteristic of this specimen is the ossified supra-spinal ligament, perfectly preserved in one of the specimens. As it was said above, this element has been preserved only in two distinct forms of titanosaurids, it is unknown in other sauropods. Although this ligament was destroyed at both ends it is clear that it extended much further than it was preserved, surely reaching the spines of the last dorsal

Titanosaurinae indet. ‘Series B’ of Peirópolis, Brazil															
Caudal Vertebrae															
Length	10.5	10.0	—	—	—	—	—	—	—	—	—	—	—	—	—
Length without posterior articular condyle	7.5	6.5	7.5	7.5	7.2	6.6	7.0	7.0	6.8	6.4	6.4	6.0	6.0	6.0	6.0
Total height	20.5*	20.0*	18.0	19.5	18.2	18.5	17.0	15.5	15.0	14.5	13.0*	11.0*	13.0	12.0	11.7
Minimum width of the centra	8.2	6.0	5.0	4.0	3.8	4.0	3.2	3.0	3.0	3.3	3.3	2.7	4.0	3.3	2.5
Height of anterior articular surface	8.5	8.5	7.5	7.5	7.0	7.2	7.2	6.5	6.0	6.0	5.6	5.5	5.3	5.2	5.0
Width of the anterior articular surface	10.4	10.0	9.3	8.2	7.6	7.0	7.2	6.3	7.0	6.5	6.5	6.0	6.7	6.5	6.0
Maximum width	23.0	21.0**	19.0	17.5	16.0	16.0	14.5	13.0	11.0	12.5*	12.0	11.0	10.0	9.5	9.0
Distance between pre- and postzygapophyses	7.2	7.6	9.5	8.1	8.0	7.4	8.5	8.3	8.3	7.5	7.0	7.2	7.2	7.2	7.2
* Measurements taken from incomplete part.															
**Measurements taken from the preserved half.															

Table 31

vertebrae. This implies limited mobility or none between the posterior dorsals and the sacrum.

Titanosauridae indet.

The specimens considered here came from several localities of Uruguay, whose data are not very precise. These sites have provided only a few fragmentary specimens. All the specimens referred to indeterminate titanosaurs from Uruguay are included in this section.

Localities.

- a) 'Estancia Las Rosas, 11 km away from Río Uruguay, in the Ineguay country (on the left bank)'. (Data from the catalogues of the Berro's collection - (MMAB 3143).
- b) Near the village of Bermúdez among the arroyos La Lancha and Maceil, 35 km from the Palmitas Station, Soriano Department, in the lands of José Gallo - (MMAB 250).
- c) Country of Cambaré, Río Negro Department - (MMAB 3602).
- d) Area between Mantas and Asencio brooks, in the lands of Morixc and Corti, near Mercedes, Soriano Department - (MMAB 4073)
- e) Arroyo Piedra Sola, near San Jacinto, Canelones Department (MHN 697).
- f) Molles, Durazno Department - (MHN 207).

Stratigraphic position. Asencio Formation (Bossi et al. 1975).

Age. Senonian, possibly pre-Maastrichtian.

Material. MMAB 4073 - an anterior caudal vertebra, MMAB 250 - anterior caudal vertebra, a fragment of the proximal end of a left tibia and unidentifiable fragments; MHN 697 - medial caudal vertebrae; MMAB 3143 - distal caudal vertebrae, MMAB 4069 - right humerus, portions of the tibia and other fragments of long bones, MHN 207- fragments of the distal end of a humerus.

Description

The above listed specimens correspond, in general, to different individuals and very probably all belong to one genus.

MMAB 4073 (Pl. 65:8). An anterior caudal vertebra in which the centrum is tall and the lateral walls are somewhat concave. The neural arch is inclined somewhat forward.

MMAB 250 (Pl. 65:6-7). Under this number we have identified a group of specimens which include an anterior caudal vertebra and a fragment of a left tibia among the determinable fragments. The vertebra is very short, somewhat taller than broad with somewhat concave, vertical lateral walls.

MHN 697 This is a poorly preserved medial caudal vertebra, which has lost the external compacta. So in this case only the anterior portion of the centrum is preserved, which is relatively short, with a prominent posterior articular cone and the apex large and somewhat elevated as in the titanosaurs. It is somewhat broader than high,

resembling in this aspect that of *Aeolosaurus*. The ventral face is somewhat concave without development of the ventrolateral crests.

MMAB 3143 (Pl. 65:9). This is a centrum of a distal anterior caudal vertebra. It is relatively tall and highly compressed, with large rectangular lateral walls, which are practically flat: this resembles the morphology of *Titanosaurus blandfordi* Lydekker.

MMAB 4069 This is a slim humerus very similar to those of the titanosaurs (except *Aeolosaurus*), a distal end of a tibia, also slender and other fragments, among which is included part of a pubis.

Comments

The centra of the caudal vertebrae have sufficient affinities with the titanosaurs of Patagonia and what is preserved is not different from many of the specimens assigned to *Titanosaurus araukanicus*. The vertebra MMAB 4073, nevertheless, is much longer and far more compressed than other known South American forms, but is similar in the morphology to the vertebrae of the Indian *Titanosaurus blandfordi*.

Elements of the appendicular skeleton are not well preserved. They are incomplete; however, we see the resemblance to the slender limbed titanosaurs. Other characters of diagnostic value cannot be distinguished.

The direct examination of the specimens in the Uruguay collections permit the amendment of the interpretations previously made by Huene (1929a and 1931), who identified these and other more fragmentary specimens as four of the species known in Patagonia, *Antarctosaurus wichmannianus*, *Neuquensaurus australis* (= *Titanosaurus australis*), *Argyrosaurus superbus* and *Titanosaurus araukanicus* (= *Laplatasaurus araukanicus*). In the author's opinion, the scarcity of specimens as well as the poor preservation of the associated specimens, impede the identification of these specimens even above the subfamily level. It is recognised, nevertheless, that among these specimens some are referable to the Titanosauridae. Indeterminate existing specimens may correspond to a large form such as *Antarctosaurus* or *Argyrosaurus*, but the only characteristic that suggests this possibility is the size, as there are no observed diagnostic morphological characteristics.

Among the specimens preserved in the Museo de Historia Natural de Montevideo and the Museo Municipal 'AC Berro' there are no identified specimens pertaining to the subfamily Saltasaurinae, which are abundant in some formations in the Neuquina Basin (Allen Formation and Río Colorado Formation) and in the Subandina Basin (Lecho Formation) corresponding to the Campanian?–Maastrichtian levels. This suggests the possibility that the Asencio Formation is somewhat older, possibly Late Campanian.

Titanosauridae indet.

Plate 17

Antarctosaurus Bonaparte and Bossi 1967.

Laplatasaurus sp. Powell 1979, pp. 193–99,
Figs 2, 3, 4, and 5.

Locality. Arroyo Morterito, at the western foothills of the Sierra de Candelaria or Castillejo, Candelaria Department, Salta Province.

Stratigraphic position. Upper section of the Los Blanquitos Formation (Pirgua Subgroup, Salta Group)—Reyes and Salfity 1973; Powell 1978.

Age. Late Cretaceous, pre-Maastrichtian.

Specimens. A group of specimens which include a left premaxilla (PVL 3670-12), a cervical vertebra (PVL 3670-13) and some caudals (PVL 3670-14), a humerus (PVL 3670-1), an ulna (PVL 3670-2), a radius (PVL 3670-3), a fragment of an ilium (PVL 3670-9), a pubis (PVL 3670-10), an ischium (PVL 3670-?), femur (PVL 3670-4), tibia (PVL 3670-5) and a fibula (PVL 3670-6/7).

Description

The premaxilla (Pl. 17:1) is high and short. Its anterolateral face is convex. Medially there is a large, flat surface which articulates with the opposite element. It has four alveoli, three of these with erupting teeth. On the ventral view, the dental foramina corresponding to each alveolus are clearly distinguished. The alveolar cavities contain three unerupted teeth, suggesting rapid dentary replacement. The teeth are cylindrical, with conical ends, slightly spatulate when unworn. The apical half has two convex faces, separated by sharp crests. Their size is appreciably larger than those of *Antarctosaurus wichmannianus*.

The humerus (Pl. 17:3) is incomplete, and affected by abrasion at both ends. This is a long and relatively narrow bone, somewhat compressed in the anteroposterior direction.

Two poorly preserved ulnae (Pl. 17:2; right and left), probably belong to the same individual. They are straight bones, robust at the proximal end. The faces are somewhat concave above; this character is lost at the distal end. The radial face has a longitudinal crest 15 cm long which corresponds to a muscle insertion.

The radius (Pl. 17:4) is long, slender and straight.

A badly preserved fragment of a left ilium is available. It has a part of the pubic peduncle and a portion of the preacetabular lamina, which is directed forward and outward. The rear of the peduncle which forms the edge of the anterior and upper part of the acetabulum, is characterised by a regular concave shape. With reservations, Powell (1979) assigned to this group an incomplete pubis, which has the greater part of the lamina preserved. It has a very obvious longitudinal swelling over the posteroventral face. The proximal part of the anterodorsal face is convex in the transverse direction,

changing to concave on the internal side. The femur (Pl. 17:7) is long, very straight, slender and anteroposteriorly compressed. The fourth trochanter is not very prominent, it is located above the posterior face, obliquely situated without reaching the medial edge and it is a little above the middle of the bone. The tibia (Pl. 17:5) is a long and flattened specimen very badly damaged at its ends (Powell, 1979). Above the medial face you can see a large groove, which goes over the proximal middle of the bone above the enmial face. There is an almost complete right fibula (Pl. 17:6) and the distal third of a left. This is a straight, thin, laterally compressed bone, expanded at both ends. The lateral face has a longitudinal elevation placed obliquely, high anteriorly and low posteriorly, where it meets the lateral tuberosity which is poorly preserved. The medial face is concave, a condition which is accentuated at the distal end.

The vertebral elements are few and badly preserved. We have identified a cervical and some caudal vertebrae. The cervical vertebra is opisthocoelous, its centrum is long and low. The postzygapophysis is partially preserved. The diapophyses and parapophyses project laterally with broad laminae. The shape of the anterior end (PVL 3670-14) is procoelous, the centrum is somewhat laterally compressed. The neural arch is short, located far forward above the centrum.

Comments

The characteristics of the caudal vertebrae, procoelous and with short neural arches located on the anterior half of the centra indicate titanosaurid identity. Reexamination of the specimens indicates that they resemble those of a tall, medium to large dinosaur, such as *Antarctosaurus* and *Titanosaurus*. Their size and general morphology clearly differ from that of *Neuquensaurus* or *Saltausaurus*, both smaller, with more robust limbs. The index of robustness of the humerus is similar to *Antarctosaurus* and *Titanosaurus*, differing from *Argyrosaurus*. The radius has strong affinities with *Titanosaurus* by its sigmoid contour, the anterior projection of the proximal end and the oblique edges of the face of the radius. These details can also be seen in *Saltausaurus* and *Neuquensaurus*, although the proportions of the bones are shorter and more robust.

The femur has morphological characteristics which resemble *Neuquensaurus*. It cannot be adequately compared with the features attributed to *Titanosaurus* owing to its poor preservation. The proximal half of the femur of *Argyrosaurus superbus*? shows notable differences in the details of the posterior face which prevents the reference of this specimen to that genus.

The relative position of the fourth trochanter resembles that seen in *Neuquensaurus*, *Saltausaurus* and *Antarctosaurus*, differing somewhat from the femora assigned to *Titanosaurus* in this aspect. The fibula is somewhat similar to those of the *Saltausaurus* and *Titanosaurs*, showing an oblique orientation of the insertion area.

The material considered above, with the exception of the premaxilla, radius, tibia, ischium and ilium, was assigned to the genus *Antarctosaurus* by Bonaparte and Bossi (1967), and to *Laplatasaurus* (Powell 1979). The morphology and proportions suggest that this material is probably more closely related to *Titanosaurus*. The caudal vertebrae have the pattern present in material referred to that genus. Present knowledge suggests that this material be regarded as Titanosauridae indet.

VI. BIOMECHANICS

The biomechanics of extinct forms, especially some large groups such as dinosaurs, pterosaurs and ichthyosaurs is not merely an intellectual exercise but a vital working tool which allows us to interpret or infer important aspects of the biology of animals not represented in the extant fauna.

Many of the interpretations coming from these studies are based on the fact that physical laws force similar adaptive solutions both in extinct and living forms, resulting in convergent evolutionary results. In this way these, convergent adaptations can be interpreted, according to the significance which they have in some of the living forms (Coombs 1975).

Some titanosaurids, like the rest of sauropod dinosaurs, reached gigantic size, becoming the most voluminous and heavy terrestrial tetrapods that ever lived. Their huge weight must have been supported by skeletons composed of the same bone material of the rest of the tetrapods, forcing the development of effective mechanical structures, in a way that could adequately support the forces resulting from great body mass.

Several authors have analyzed mechanical aspects in tetrapods, outstanding among these being d'Arey Thompson (1942), Slijper (1946), Hildebrand (1974). Coombs (1975) and Alexander (1989) paid special attention to the biomechanics of sauropods. The former includes an extensive bibliography concerning the subject.

All of the great terrestrial tetrapods have been exposed to a series of biomechanical problems owing to their great size and weight. These animals developed a series of morphological and postural adaptations which contributed to effectively supporting this weight. They are called graviportal. As pointed by Hildebrand (1974), those special structures and postures of graviportal animals avoid unnecessary oscillations and jolting. Limbs are little flexed during locomotion. There is a tendency to avoid shearing forces in long bones, and to turn them into compressive ones through the development of straight columnar limbs. Consequently, the mechanical properties of the bone are optimised, resulting in a greater efficiency. Experimental tests show that the resistance to rupture in compact bone tissue is greater when compressed than when sheared (Hildebrand 1974).

Sauropods including titanosaurids, show some of the adaptations characteristic of graviportal animals (Coombs 1975).

A. SKELETON

For a better understanding of the form and biomechanical behaviour of titanosaurids, it is convenient to first present a general analysis of the skeleton.

One of the comparative models suggested for the interpretation of the mechanical functioning of a vertebrate is that of a cantilevered bridge. The fore and aft limbs act as pillars held together by the roadbed (trunk's axial skeleton), and the neck and tail are flying beams. In this model, the compressional element is the roadbed (the centra) above which there are tensional elements: the cable and cross bars (mechanical complex integrated by the apophyses, epaxial muscles and intervertebral ligaments). The whole structure is based on four points, although in the present case, these are dynamic.

A more appropriate analogy is the one suggested by Slijper (1946) who pointed out that the axial skeleton operates as a system of bows and strings. In this model, the axial skeleton operates as a bow, and tendons ligaments and muscles as strings; e.g. in the trunk the bow is represented by vertebrae and the string by the abdominal and other ventral muscles. In this model the bow (segments of the axial skeleton) is the compressional element and the string, the tension. The suspension of the head and neck can be likewise explained since the cervical region and the anterior dorsals form a bow ventrally convex, with its string constituted by the nuchal and other intervertebral ligaments.

However, the proposed models are valid for static structures, and likewise, its functioning would undoubtedly be far more complex in the case of non-static terrestrial tetrapods.

1. Skull

There are very few known titanosaurid cranial remains. The most frequently preserved part of the skull is the braincase, in which the biomechanical elements are few, since its anatomy is quite conservative. The presence of long paroccipital processes in *Antarctosaurus* and *Saltasaurus*, which apparently constitutes a synapomorphy of titanosaurids, allow us to infer some peculiarities in the functioning of the jaws. The depressor muscles are inserted on these processes. It is valid to point that these processes were also very well developed in hadrosaurs, whose jaws were highly specialised for efficient chewing (Ostrom 1961, 1964). However, the two groups have completely different teeth and occlusal patterns. In any case, prominent paroccipital processes could be related to some kind of effective plant cropping.

Very little is known about titanosaurid jaws. *Antarctosaurus*'s jaws, described in Chapter V, have a characteristic 'flat shovel' shape. It is very low and

different from those known in other sauropods. This peculiar morphology must be related to specialised feeding habits. The anterior region is broad and ventrally flattened. It could be linked to some feeding resource, immediately above a plane surface, such as low vegetables on the ground or floating plants in water. The first possibility does not fit, at first glance, with long necked sauropods such as *Diplodocus*, *Brachiosaurus* and *Apatosaurus*, with long cervical vertebrae which parallel giraffe's feeding from the tops of trees. However, not all titanosaurids have very long necks (e.g. *Saltasaurus* and *Neuquensaurus*), and undoubtedly could feed on other vegetation levels. In the case of *Antarctosaurus*, there are no known cervical vertebrae.

Antarctosaurus in particular must have been of considerable height, a feature usually related to a folivorous diet. However, the teeth are small both in size and diameter, suggesting the possibility that instead they fed on soft vegetation, such as aquatic plants (e.g. *Salvinia*, *Eichornia* and *Pistia*), some of which existed during the Cretaceous (Krassilov 1981).

The morphology of a premaxilla assigned to Titanosauridae indet. from the Los Blancos Formation (Salta province, Argentina), previously described, allows the inference of a rather high, strong and narrow snout with cylindrical, slightly spatulate teeth. The latter are thicker than those of *Antarctosaurus*, and had a high rate of replacement. This would probably allow them to make a more efficient use of harder plants.

2. Axial skeleton

The vertebral centra show adaptations which allow them to deal with the problems presented by gravity to an animal of such great size and weight. Titanosaurids have solved part of these problems by developing low density elements that are highly efficient mechanically. They were models of structural optimization, partially different to those known in most of the sauropods.

The cervical, dorsal, sacral and in some cases, caudal vertebrae of titanosaurids are not entirely solid, but partially constituted of cancellous tissue. The same applies to some thick structures such as the neural spine, diapophysis, parapophysis, etc. paralleling in some way the specialization observed in some theropods (Bonaparte, pers. comm.). These adaptations have been critically analyzed by Coombs (1975). Originally they were interpreted as air sacs, and afterwards as pneumatic floaters. Others, finally, suggested them as a means to make these elements lighter. If instead of air these cavities were filled with fat or lax connective tissue, then they would have served the same purpose (Coombs, op. cit.). The cervicals progressively increase in size towards the base of the neck, as an answer to the progressive increment of compressive forces, generated by the head's weight, the anterior vertebrae and the muscle strength. Titanosaurid cervicals do not have the wide and well defined pleurocoels seen in other Jurassic sauropods

(Diplodocidae, Camarasauridae and Cetiosauridae). At first sight, this suggests they are primitive in this aspect of the structure of their cervical centra. The centrum is basically formed by two thick laminae making the diapophysis and parapophysis quite flat, joining and widening medially to form the articular surfaces. All of the vertebral body, diapophysis, prezygapophysis, postzygapophysis and neural spine, possess the cancellous structures characteristic of the family.

On the dorsals, there are structures related to the solution of gravity problems. These have been enlarged as an effective response to the mechanical requirements imposed by the increase of body volume. To make this possible without considerable weight increase, optimised vertebral structures have developed, where the bone material involved is reduced to a minimum, without loss of the needed mechanical efficiency.

On the dorsal centra, as has been presented in the descriptive section of this work, the ample pleurocoels present in other sauropods are missing. Instead, they have cancellous tissue in which the cells are oriented with the major axis following the direction of the compressive forces to which the vertebral centrum is usually subjected. This condition is similar to that which occurs in the trabecular orientation of other vertebrate bones (Hildebrand 1974).

Except for the laminae located on the main axis (prespinal and postspinal) which are usually little developed in titanosaurids, the rest have additional functions, related to other structures such as reinforcement (spinopostzygapophysial)

The diapophysis, besides the functions related to the transmission of force (capitulum) are, as well, beams subject to flexion through the action of muscles and ligaments, and have developed as a light structure to render these functions with the least possible weight. Normally, they have a 'T'-shaped section at the proximal end of the ribs.

Postzygapophysis are normally fixed to the neural spine through the spinopostzygapophysial lamina. Prezygapophyses and parapophyses are part of the same body on the medial dorsal and posterior vertebrae, which is held by the neural arch whose cancellous tissue is the same as that of the vertebral body.

Titanosaurids do not show the additional articular system achieved by other sauropods, which is known as hyposphene-hypantrum. An exception is the titanosaurid *Epachthosaurus sciuttoi*, which does possess a thin accessory articulation.

The sacral ribs show adaptations which have led to structural optimizations. They had a section that resembles I-shaped structural profiles, formed by a lamina enlarged at the upper and lower edges, where the

compressive efforts are concentrated upon the upper edge, and the traction on the lower. The laminae between these two edges is called the beam's alma, which is not subject to significant forces. For this reason there can be one or two windows placed at points which do not compromise the structural integrity of the sacral ribs. Because the sacral ribs transmit close to half of the body weight, we can presume that their light structure would have been arranged in such a way that their laminae were parallel to the gravity force.

If the pelvis is oriented using this criteria, as was done experimentally with PVL 4017-92, the sacrum's axis would have had an approximate inclination of 25°. An ossified tendon is present in *Epachthosaurus sciutoi*, and in material assigned to Titanosauridae indet. from Peirópolis (Brazil), in the former extending forwards reaching the last dorsals. Its presence allows the deduction that these dinosaurs had a restricted mobility at the posterior end of the trunk, coincident with the tendency of a somewhat rigid axial skeleton in graviportal tetrapods (Hildebrand 1974). This ligament would have worked in the same way, as the 'cable' does in 'Cantilever' bridges, resulting in an economy of material and weight as well.

The procoelous condition of the caudal vertebrae in titanosaurids has been noted by most of the scholars since the first discovery of the family. It is worth analysing the advantages of this condition from the biomechanical point of view. A ball and socket articulation is a derived character in dinosaurs, which allows a wider range of movements that are solely limited by the action of the zygapophyses. Troxell (1925) has analyzed the biomechanical characteristics of crocodilian vertebrae (Eusuchia). In this sense, when forces are transmitted through the tail towards the head (such as is the case where it is used as a support), the procoelous centra would result in a much more efficient articulation than opisthocoelous ones.

Forces are transmitted through each vertebra in the direction of the major axis of its centrum, and its resultant is normal in relation to the centre of the convex surface. Stated differently, this effort is transmitted to the convex surface of the immediately preceding element falling at an angle relative to its axis, but supported by the massive extent of the convexity.

In the opposite case, (opisthocoelous) the force is transmitted from the convexity towards the concavity, which if it is at an angle relative to its axis, the latter is more prone to failure, tending to fracture the edge of the capsule. This interpretation is in concordance with the sauropod fossil record, because in the Late Cretaceous taxa having ball and socket articulations, the procoelous condition is far more frequent than the opisthocoelous one, with the only exception being *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka 1977).

3. Scapular girdle and forelimbs

At the beginning of the twentieth century, various scholars held the theory that the forelimbs of sauropods were oriented in a fashion similar to that of extant crocodiles where the position of the articular facets, is not clearly defined. With the discovery of articulated material of *Camarasaurus* it became evident that sauropods had a similar posture to extant elephants (Coombs 1975). Sauropods would have been very slow owing to the short lever arm, and the relative immobility of the pectoral girdle as a result of the presence of large ventral elements. Coombs (1975) suggest even slower movements than in elephants. The scapula of *Saltasaurus loricatus*, oriented in the position previously discussed, is characterised by having the glenoid articular surface basically forwardly oriented. The articular surface of the coracoid faces outwards and backwards. Although the lack of preservation of the articular cartilage makes it is hard to interpret correctly the functional significance of this articular surface morphology, it can be presumed to indicate at least some ability to make humeral movements in an oblique plane (anteromedial to posterolateral), in relation to the sagittal direction.

The ulna and radius are basically straight, which means it is unlikely that the two bones ever crossed over one another. According to the preserved articular surfaces, it can be inferred that the radius would be in front of the ulna at both its proximal and distal ends. In this way, the metacarpals would have been vertically placed, forming an arc as is common in titanosaurids and other sauropods (Huene 1929a; Gilmore 1946 and Borsuk-Bialynicka 1977; Upchurch 1994). In this way the palmar side of the manus would be medially and posteriorly oriented. Such an orientation is present in *Alamosaurus sanjuanensis* (Gilmore 1946), *Epachthosaurus sciutoi* (Powell 1990) and *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka 1977). The claw of digit I is not documented in articulated titanosaurid remains. However its presence is indicated by the finding of isolated claws in bone accumulations where titanosaurids are the only sauropods present.

4. Pelvic girdle and hindlimbs

Titanosaurids, in which the pelvic morphology is adequately known, as in *Saltasaurus loricatus* (Pl. 31 and 55:6,7 and 8) and the documented forms of the Bauri Formation in Brazil (Pl. 16:1,2 and 3), show that they possess a strikingly broad trunk, a character clearly obvious owing to the curving of the ribs of the first sacral vertebrae (sacralised dorsals), which are attached to the anterosuperior edge of the ilium of the pelvis (Pl.16:2a). Although there are no known anterior dorsal vertebrae with their corresponding ribs, which might allow one to establish an adequate morphology of the thorax, it is highly probable that it was quite broad as well. Bakker (1971) argued that amphibious tetrapods, are mainly barrel chested, while terrestrial ones show taller and mediolaterally compressed thoracic sections such as in *Apatosaurus*. The mechanical characteristics of both thoracic morphologies have been debated by Coombs

(1975), who concludes by pointing out that because the sauropods have the modifications that can be expected in strongly terrestrial animals, it would be reasonable to conclude that they regularly inhabited (if not exclusively) terrestrial environments. In the particular case of *Saltasaurus loricatus*, we can test whether these interpretations follow. As mentioned in the descriptive section, this titanosaurid was a medium size sauropod, rather short and robust, with a very broad trunk, almost cylindrical at the back. Evidence for this character is the existence of a broad pelvis with laterally expanded iliac laminae. The analysis of similar Brazilian elements shows that the dorsal vertebral ribs were very expanded laterally, and it is highly possible that this characteristic might have extended, perhaps in a lesser degree, to the rest of the trunk.

The trunk's morphology in titanosaurids (*Saltasaurus loricatus* and *Neuquensaurus australis*, *Aeolosaurus rionegrinus* and other undetermined forms from the Brazilian Baurú Formation) would appear to differ somewhat from what is common in sauropods, approaching to some degree what is common in some mammals of amphibious habits. According to the available evidence, the hind limbs of titanosaurids were of the plantigrade type. As for the forelimb, the long bones are quite straight, a condition which allows a more efficient support, by eliminating most of the shearing forces (Hildebrand 1974). The acetabulum's articular surface is mainly formed by the ilium and the lower distal expansion of the sacral ribs. Compressive forces upon the femur are supported by the ilium. This kind of adaptation is present in some sauropods as *Haplocanthosaurus* (Hatcher 1903) and *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) being a titanosaurid characteristic. It represents a double biomechanical advantage: enlargement of the area of effort transmission in the articulation, resisting the force by unified surface, and diminishing or eliminating the shearing forces between the sacral ribs and the ilium. This function is, besides, assured by the coossification of both elements (Pl. 75, 83). The outline of the iliac portion of the acetabulum has a parabolic shape with its apex near the base of the pubic peduncle. This structure is a strong and wide process ventrally oriented which limits the forward movement of the femur.

Plaster casts were made to understand the functional significance of this character of *Saltasaurus loricatus*, and later used to recreate the movements with different sacral angles. When the sacrum's axis is in a 45° position in relation to the horizontal, the movement angle of the femur in relation to the vertical, is more or less the same fore and aft. With this sacral angle, and the femur in vertical position, the force lines would go through the apex of the parabola determined by the acetabular outline. Because a 40° angle of the sacrum's axis would perhaps be excessive for this sauropod on all four limbs, since it would result in a strongly curved column in the dorsal region, it is possible that this morphologic condition was

a useful adaptation when the animal stood on its hind limbs to feed.

Borsuk-Bialynicka (1977) proposed for *Opisthocoelicaudia skarzynskii*, which has a similar morphology, an occasional bipedal habit, pointing out the similarity that sauropods had with the megatheres in the strongly ossified pelvic structure and with greatly expanded ilia and very robust tail. Bipedal habits or some kind of 'tripodal' stance have been also suggested by several authors (Osborn 1899b; Riggs 1904; Coombs 1975; Norman 1985; Bakker 1986; Powell 1986; Jensen 1988 and Upchurch 1994). Borsuk-Bialynicka (1977) suggests the possibility that this particular morphology of the ilia is an adaptation for supporting the viscera when the animal adopts a bipedal position, and facilitates lateral movements for other body parts. Although this hypothesis has not been rejected, this peculiar morphology has other major functional implications as well.

Nevertheless, the idea of a functional convergence in the pelvic structure of the megatheres and sauropods such as *Saltasaurus* and *Opisthocoelicaudia* is an accurate and remarkable conjecture. In *Saltasaurus* and other titanosaurids a series of adaptations which imply a similar biomechanical hypothesis are present as well. Among them the possession of a strong pelvis could be cited, characterised by a notable co-ossified sacrum, fused sacral ribs and ilia, laterally expanded laminae, and a robust anterior portion of the tail, which probably functioned as a tripod for the adoption of a bipedal posture.

This hypothesis is consistent with other facts. The presence of a highly developed 'claw' on digit I, is interpreted as a structure probably related to tree trunk grasping during high browsing (Upchurch 1994), and not for defence. Otherwise, most of the weight of *Diplodocus* and *Apatosaurus* was supported by the hind limb, bringing the centre of gravity backwards, close to the pelvis (Alexander 1989).

If the pelvic expansions have some relation with the capacity to assume a bipedal posture, the probable function should aim at a study of the biomechanical implications of the musculature. According to the interpretation emphasised by Romer (1923), the muscles which originate in the pre-acetabular area, on the external face of the ilium, are the *iliofemoralis* and the *iliotibialis* (Pl. 84). Although a change in the area of origin of these muscles occasionally modifies their effectiveness, this structure does not result in an important biomechanical advantage for a bipedal walker.

Although the muscles have this relationship to the ample anterolateral projections of the ilium in megatheres, it is not present in the anatomy of living edentates. Slijper (1946) illustrated and discussed the position and characteristics of the epaxial muscles. As indicated in *Dasypus novemcinctus* (Pl. 85), the *iliocostalis lumborum* muscle originates on the metapophyses of the last ribs, transverse processes of the sacral vertebrae and mainly on

the ilium. This same author indicates that the *longissimus dorsi* has a marked tendency to fuse with the *iliocostalis lumborum* to form a single muscle: the *erector spinae*. This combined muscle is related, in the mammals, to the movements in the parasagittal plane.

Owen (1842) in the study of *Myiodon robustus*, supposed that the expansion of the ilia was related to the insertion of the epaxial muscles which was in turn related to the sagittal movements of the trunk, an interpretation which agreed with the observations made later by Slijper (1946).

The development of the muscular system resembling the above description, being very effective in sauropods for an occasional bipedal posture was probably adapted for eating, while the ilia functioned as a long strong lever for the epaxial muscles, which effectively controlled the sagittal and lateral movements of the presacral region.

B. FEEDING HABITS

Traditionally diverse forms of herbivorous habits have been assigned to sauropods, but there is little direct evidence concerning their diet. Stokes (1964) found fossil vestiges interpreted as the stomach contents of a Jurassic sauropod from the Morrison Formation of the United States. It was an ovoid body, where the original form is not perfectly known because it was partially altered when found. Polished surfaces of this material indicated vegetation fragments without preferential orientation, consisting of pieces of twigs 2.5 cm. long x 1 cm in diameter, although crushed, with a series of characteristics which clearly differentiated the vegetable specimens from transported material. Moreover, bone fragments were found, for which Stokes (1964) has suggested the possibility of omnivorous habits in sauropods. [Editor's note: This is now known (although not yet published) not to be gut contents (James Madsen, pers. comm. to Ralph Molnar)]. Otherwise there exist only various hypotheses concerning the diet of these dinosaurs based on analysis of their dentition.

There are two main types of teeth among the sauropods: the spatulate or 'camarasauriform' with a surface of wear more or less perpendicular to the axis of the tooth, and the cylindrical or 'diplodociform' with strongly beveled wear facets.

The former are present in the 'Cetiosauridae', Camarasauridae, Brachiosauridae and Euhelopodidae. The latter are present in Diplodocidae and Titanosauridae.

Cylindrical teeth are present in derived 'diplodocoid' skull patterns. The dentition is limited to the anterior part of the snout: premaxilla, anteriormost part of the maxilla and anterior part of the dentary. Teeth are slightly spatulate when unworn. Worn teeth bear beveled wear facets suggesting a kind of shearing action for cutting, an effective adaption for the herbivorous diet (Powell 1986; Barret & Upchurch 1994). Calvo (1994b) recognises two different patterns of the 'cylindrical' teeth. The peglike teeth included *Diplodocus*, *Apatosaurus*, *Dicraeosaurus*,

Amargasaurus. The chisel-like tooth characterise *Titanosaurus*, *Antarctosaurus*, *Nemegtosaurus*, *Quaesitosaurus* and *Saltasaurus*. However, the classification proposed by Calvo (1994b) seems to be weakly supported by available evidence.

As mentioned in the descriptive section, known titanosaurid teeth are very small in relation to the body size, generally cylindrical in form, and somewhat compressed labio-lingually in the apical part of the crown. When unworn, they show a slight degree of 'spatulation'. New evidence indicates that some titanosaurids could also have another tooth pattern that needs to be verified by the discovery of teeth in situ in undoubted titanosaurid bones. The first of the above type was described by Jacobs et al. (1993), for the African Early Cretaceous titanosaurid *Malawisaurus*. The second was indicated by Le Loeuff (1995) and assigned to the French Late Cretaceous titanosaurid *Ampelosaurus atacis*.

The most common peg-like teeth bear flat, oblique wear facets. The latter incline between 90° and 23° in relation to the tooth's axis, which suggests tooth against tooth friction in the course of food processing. The strongly inclined wear facet planes were interpreted as related to some kind of cutting action (Powell 1986). This hypothesis accords with studies by Calvo (1994a), who found microwear expressed by longitudinal scratches almost parallel to the tooth axis.

There are various interpretations concerning the position and functional meaning of tooth wear facets. Barret and Upchurch (1994) concluded that *Diplodocus* has labial wear facets both in the upper and lower teeth, explaining some exceptions as incorrectly repaired elements. Calvo (1994b) described labioventrally facing wear facets for *Diplodocus*, and linguodorsally facing wear facets on the lower dentary elements. I personally agree with the illustration presented by Calvo (1994b; Fig. 1b), which indicates that the axes of upper and lower teeth are slightly irregularly oriented and consequently determine variations on the wear facet's development and orientation. This interpretation is consistent with titanosaurid teeth found at the Late Cretaceous Allen Formation at Lago Pellegrini (Río Negro Province) characterised by having two wear facets: a new one superimposed on an older one.

Spatulate teeth, otherwise, occur in skulls whose dental row is extended backwards, approximating in part those found in prosauropods, which have spatulate teeth.

These observations permit the inference that probably the spatulate teeth constitute a primitive form, while the cylindrical ones represent a derived character, developed independently in diplodocids and titanosaurids.

The camarasauroid morphology, nevertheless is much more cylindrical as seen in *Camptylodoniscus ameghinii*.

The maxilla of *Campylodoniscus*, assigned with doubt to the Titanosauridae, has a different tooth pattern. They are more spatulate than most of the titanosaurs, with a more inflated crown, and a strongly convex labial face. This shape is more related to that of *Camarasaurus*, which usually exhibits wear facets developed perpendicularly to the tooth's axis or 'parallel to the labio-lingual axis' as expressed by Calvo (1994b). The position of the alveoli indicate a dental series which extends back on the maxilla as in the camasauroid skulls, not anteriorly restricted as in *Diplodocus*, and probably *Antarctosaurus* (Powell 1986; Calvo 1994b). This second type or pattern of teeth suggests a crushing and cutting function (Powell 1986; Calvo 1994a). With a cranium similar to *Camarasaurus* in having a somewhat elongated tooth row, cutting and probably a partial trituration is also suggested for *Campylodoniscus*.

The morphological characteristics of the teeth, as well as their position in the mandible, are known in the titanosaurs only in *Antarctosaurus wichmannianus*, which generally resembles the diplodocoid pattern.

The latter, whose skulls and dentitions are better known, have been interpreted as having a soft vegetable diet (for example algae, Hay 1908) and soft shelled invertebrates (Haas 1963). The presence of wear facets, and the fact that teeth are not smaller than incisors of mammalian browsers or grazers led Bakker (1971a) to infer that this sauropod probably had similar habits. The lack of dentary elements specially adapted for crushing does not exclude the latter interpretation since this process could be accomplished in the digestive tract, through a mill of swallowed small gravel (gastroliths) as suggested by several authors and summarised by Calvo (1994a), as in the gizzard of the birds or the stomachs of some crocodiles (Bakker 1968). Chemical or bacterial disintegrating action could also have occurred (Coombs 1975).

Many of these interpretations, based on dinosaurs of 'diplodocoid' type, may be extrapolated at least to some titanosaurs, characterised by a similar organization. During the Late Cretaceous, as has previously been mentioned above, an important radiation of the angiosperms occurred, some of which invaded the aquatic environment, as did some ferns. Both could have served as a food for some titanosaurs in a tropical and subtropical climate, as has been suggested by Krassilov (1981).

The mandible with a 'broad and flat scoop' shape of *Antarctosaurus wichmannianus*, suggests the possibility that this titanosaur obtained its food very close to a flat surface: (as even over the soil or close to the water surface).

It is very probable, nevertheless, that titanosaurs had diverse feeding habits. Both their taxonomic diversity and differences in morphology and teeth size suggests this. Titanosaurid diversity is probably related to their late appearance, and scarcity during the Late Cretaceous in

South America of ornithischians and other large herbivores.

C. BODY TEMPERATURE AND ITS REGULATION

For a long time dinosaurs were considered to be ectothermic as are living reptiles. Over a time span of little more than a decade some investigators, outstanding among whom are Russell (1965), Bakker (1971a, 1971b, 1972a, 1974), Ostrom (1974) and Desmond (1975), pointed to a series of factors supporting the hypothesis that dinosaurs were endotherms, as are birds and mammals.

The principal evidence pointed out by the defenders of this theory were the erect position of the legs and the possibility of reaching considerable speeds in some groups, thanks to their particular biomechanics, internal nares located somewhat farther back than is common in reptiles (the structure which permits a more efficient mastication), the presence of supposed air sacs within the vertebrae of sauropod and theropod dinosaurs; the microscopic structure of the bones, similar to that of mammals with a well developed Haversian texture and predator claws similar to those of mammals (Bakker 1972).

This interpretation prompted an important and productive discussion which led to a much delayed analysis of many aspects of the anatomy, physiology and taphonomy of reptiles and mammals including fossils and living animals, from which an interesting series of conclusions resulted.

A brief but sufficiently complete critical review of this problem was carried out by Benton (1979). This paper includes an extensive bibliography on the subject.

I shall comment below on the most outstanding characteristics of the large dinosaurs, particularly sauropods, in this regard. Among the most outstanding factors in the consideration of body temperature of sauropods and its regulation are: the great volume which is characteristic of them and its influence on the mechanism of heat dissipation, as well as the amount of food necessary to maintain its biomass, the characteristics of the bone histology and the size of the brain.

1. Size and body temperatures

Large size in many groups of dinosaurs, and particularly in sauropods, is one of the most interesting attributes to consider in relation to body temperature and its regulation. Bakker (1972, 1974) asserted that all dinosaurs, regardless of size, were endothermic, with a standard high metabolic rate and consequently with high body temperature. In the case of sauropods, Bakker (1974) concluded that air sacs indicated a probable unidirectional flow of air through the lungs, with a great capacity for aerobic metabolic activity as in the birds. Nevertheless, these could be adaptations to reduce the weight of the axial skeleton, which is seen not only in the

centra, but also in all of the vertebrae (including the neural arch) where most sauropods developed very light but sound and efficient biomechanical structures.

Other consequences of weight increase in sauropods is the limitation preponderantly to a slow walking gait, which does not require a high metabolism and which is not an important source of heat.

One of the fundamental factors is the reduction of the surface/volume ratio as body size increases. In other words, reduction of the relative amount of surface through which the heat exchange is performed (passive loss or heat gain) as body size increases. Heat exchange happens through convection, radiation and conduction, and the rate per unit of body mass declines as volume increases (Shmidt-Nielsen 1976).

There are various studies concerning heat exchange in large living reptiles such as crocodiles (Colbert et al. 1946), the lizard *Varanus komodoensis* (McNab & Auffenberg 1976) and the Galapagos turtle *Geochelone elephantopus* (Mackay 1964).

These studies show that the exchange of internal body heat which occurs in subtropical regions with normal temperature fluctuations, is very slow.

In the case of *Geochelone elephantopus*, Mackay (1964) has demonstrated that it maintains its body temperature very nearly constant, varying only about 3°C in the body core, in a daily ambient fluctuation temperature of 20°C.

Spotila et al. (1973) analyzed heat transfer data on crocodiles simulating a relatively small dinosaur 1 m in diameter. He deduced that with a daily fluctuation of about 22°C, the model would be able to maintain a body temperature between 28.5°C and 29.6°C.

Based on this analysis, sauropods, as the largest dinosaurs in the equable Jurassic and Cretaceous climates, could maintain a constant body temperature with very small variations (2°C), without an endogenous heat source (Colbert et al. 1946; Benton 1979). Additional heat could be added by fermentation processes (Dodson 1990).

In this manner, the sauropod dinosaurs and therefore, the titanosaurs, were animals with undoubted ectothermic characteristics with homeothermal inertia, enjoying the advantages of homeothermy, without the energy costs of endothermy. Spotila et al. (1991) in Fastovsky and Weishampel (1996) proposed the term gigantothermia for large dinosaur which implies 'mass homeothermy' and a certain control of blood circulation in peripheral tissues to dissipate heat excess.

2. Bone-histology

Titanosaurids show a profuse development of the Haversian system in the compacta, similar to large mammals. This type of texture is also seen in the long bones of other dinosaurs (Enlow & Brown 1957; Ricqlés

1974 and references therein). Reid (1981) observed a different pattern, a laminar vascularised structure in sauropods, with lines of arrested growth. These lines are interpreted as being a consequence of seasonal decreases in growth rate. This pattern indicates that growth is somehow related to seasonality (Fastovsky and Weishampel 1996) as would occur in an ectotherm. Although the ischium of *Saltasaurus* has a highly developed Haversian system, dermal ossicles show several lines of arrested growth. These structures are also present in the enamel of titanosaurid teeth.

Bakker (1972a) generalised by saying that in mammals, bone is characterised by an abundant vascularization and a profusely developed Haversian system, although in living reptiles the compacta has little or no Haversian systems. These observations led Bakker (1972, 1974) to infer that dinosaurs, by possessing this type of histology, were endothermic as mammals.

Bakker's hypothesis has been refuted among others by Bouvier (1977), who indicated through various examples, that there exist many mammals which lack the Haversian systems or show scant evidence of it and that something similar occurs in many birds. Reptiles show a range of variation in the development of Haversian systems similar to mammals. Haversian systems are present in certain reptiles, amphibians, and fossil fish as well as in some extant turtles, while endosteal Haversian systems are present in Chelonia, Squamata and Crocodylia (Bouvier 1977).

The Haversian system, strongly developed in dinosaur bone, is interpreted as a structure related to rapid growth (Ricqlés 1974), and is generally associated with large size (Halstead 1975). Otherwise, the development of Haversian systems apparently is related to increased bone stress (Martin 1979).

3. Brain and body weight relationships

Hopson (1980) analyzed the encephalisation quotient (EQ) in dinosaurs and its implications in the interpretation of body temperature and its regulation in dinosaurs. According to his observations, sauropods, ankylosaurs and stegosaurs are the dinosaurs with the lowest EQ. These groups are within the range of living reptiles in this respect, which reflects low metabolic rates. This is consistent with the low speed of locomotion, limited agility and activity, inferred for titanosaurids.

4. Food requirements and their implications in the interpretation of thermal regulation in sauropods

According to the known data concerning daily energy costs in living endotherms, (mammals), and ectotherms (reptiles), for the same biomass (McFarland et al. 1979) the daily energy cost of a 1 kg endotherm is the same as that needed for two ectotherms of the same weight. According to the results presented, the relation of energy requirements per/animal/per/day for a body mass of 1000–10 000 kgm is of 10:1 (mammal/reptile).

To analyze the paleoecology of the dinosaurs of Tendaguru, Beland and Russell (1980) remarked that a large endotherm—such as a 1400 kg elephant—consumes about 60 kg of fresh vegetation per day over a time span of 19 hours, while a 15 ton sauropod consumed the same amount of vegetation, which is tentatively close to the maximum limit of the biomass. Otherwise, it is difficult to conceive of an endothermic sauropod with a cranial specialization similar to *Diplodocus*, (whose skull size is not very different from that of a horse), which supported a biomass of 15 tons ingesting 600 kgm of fresh vegetation daily using a 'reaping and harvesting apparatus' of a size and efficiency not much more than a horse's. Dodson (1990) takes a different approach to estimating sauropod's food requirements, considering the caloric value of potentially ingested plants. He summarises several studies indicating that relatively small sauropods could be endothermic by selecting high caloric-value vegetation. However, he considers that sauropods, like other large phytophagous tetrapods, were not in fact selective but ate whatever was available, including low caloric-value plants, which were probably more abundant.

All of these observations indicate that sauropods, including titanosaurs, were very probably ectothermic animals, that well might have had the benefits of the endotherms, being inertial homeotherms. In this way the high costs which are necessary for internal temperature regulation (amount of food in particular, heat dissipation, etc.) can be avoided. They are not necessary in a uniform climate (Axelrod & Bailey 1968) which was probably the case in the Cretaceous subtropics.

VII. LIST OF NON-SOUTH AMERICAN TITANOSAURIDS

(Map 16)

Titanosaurid dinosaurs, are well documented in South America, although also known in North America, Europe, Africa and India. In the palaeontological literature there are references to Asian localities from which specimens referred to this family have been cited, but based on material without diagnostic value.

A. NORTH AMERICA

In North America, there are three localities where titanosaurs are known, all of them in the south-west.

1. North Horn, Utah, United States

The most complete and significant remains from North America were found in an area south-east of North Horn Mountain, Manti National Forest, Emery County, Utah. The fossil-bearing levels correspond to the lower part of the North Horn Formation, of Senonian age. Gilmore (1946) described and illustrated a specimen discovered by George B Peace in 1937, which included 30 caudal vertebrae with hemapophyses, both ischia, right front limb, scapula, coracoid and sternal plates, assigned to *Alamosaurus sanjuanensis* Gilmore 1922.

2. Barrel Springs Arroyo, New Mexico, United States

The holotype of *Alamosaurus sanjuanensis* consists of a right scapula and a right ischium. It was found at this locality, situated 1.5 km south of Ojo Alamo, in San Juan County, New Mexico. The stratigraphic unit bearing the holotype material corresponds to the Naashoibito Member of the Kirtland Formation (Lucas and Sullivan (2000).

The specimens described by Gilmore (1921, 1922) and Mateer (1976) were obtained from a layer of white sands and conglomerates with dark concretions. Those described by Kues et al. (1980) came from a different level of thick channel deposits. The latter specimens are cylindrical teeth with wear facets typical of titanosaurs. The Naashoibito Member of the Kirtland Formation is considered Maastrichtian by Lucas and Sullivan (2000). The faunal list includes the following taxa: Theropoda indet., Chelonia indet., Crocodilia indet., Ceratopsia and Ankylosauria?

3. Big Bend National Park, Texas, United States

Lawson (1972) in Kues et al. (1980) cited the presence of titanosaurs in the Big Bend National Park, Brewster County, in west Texas, collected from the Tornillo Group.

B. AFRICA

The African titanosaurs are much older than those known in South America. Among the recovered material, some are very interesting and require special attention, but are beyond the scope of the present work. The study of these forms would surely contribute to the understanding of the early stages of titanosaurid evolution.

1. Niger

Niger has two important localities with Cretaceous vertebrates. These have yielded material assigned to Titanosauridae. These are Gadofaoua and In Beceten.

Gadofaoua is situated south-east of the mountainous Massif Lair, very close to the geographical centre of Niger (Taquet 1976). It is a very important locality which has produced the remains of plants, invertebrates and vertebrates of Aptian age. Among the latter, distinct types of fish, turtles, crocodiles, mosasaurs and dinosaurs (ornithopods, carnosaurs, coelurosaurids and sauropods). Among the specimens assigned to sauropods is a complete skeleton of a juvenile (Taquet, op. cit.) with prococious caudal vertebrae and the general characteristics of titanosaurs. Curiously, they exhibit some derived features in the centra, as in the South American saltasaurines, such as the development of cancellous tissue in addition to the notable development of lateral pleurocoels that are only weakly manifested in some Late Senonian South American titanosaurs.

A detailed study of this last form, and its comparison with others of the Late Cretaceous from other parts of the world would contribute valuable information concerning

the evolution of the group, which constitutes the most ancient of those listed from Gondwana.

The remaining locality is In Beceten. It is known from the work of de Broin et al. (1974), who has stated the general outline of the geology of the area, and briefly reviewed the fauna known from this locality. This includes fish, amphibians, squamata, chelonians, crocodiles and dinosaurs, (carnosaurs and sauropods assigned to the family Titanosauridae).

The place is in the south of the Republic of Niger, 90 km to the east of Villa de Tahona. The vertebrates are found in clays that are part of a sequences of alternating clays and calcite interpreted as corresponding to alternating continental and marine deposits (de Broin et al. 1974). Based on the recorded marine fauna, this unit has been assigned to the Early Senonian.

2. Egypt

Baharija is 250 km south-east of Cairo. It has yielded a profuse number of Early Senonian vertebrate taxa (Stromer 1932) among which there are crocodiles, chelonians, dinosaurs (coelurosaurs, carnosaur, and two different types of sauropods, one of which corresponds to a lineage related to *Dicraeosaurus*, and *Aegyptosaurus baharijensis*, the latter referred to the titanosaurid family).

3. Madagascar

The fossiliferous area which has provided remains of titanosaurids and other vertebrates in the Cretaceous of Madagascar is located in the north-west of the island, in a region situated approximately 40–50 km to the south-east of Majunga, near the Maevarana locality (Russell et al. 1976). These authors presented an historical review of the first discoveries among which were encountered the specimens described as *Titanosaurus madagascariensis* by Depéret (1896).

The rocks carrying these specimens correspond to the 'Sandstone of Maevarana' to which a Late Senonian age was assigned. They are part of a sequence of continental deposits which lie in the Majunga basin, above basalts of Turonian age (Hoffstetter 1961) and are covered by marine sediments of Early Maastrichtian age.

The vertebrates listed from these levels include fish, chelonians, snakes, crocodiles, dinosaurs including sauropods (Titanosauridae), carnosaur, and among the ornithischians, and a supposed stegosaur (Russell et al. 1976).

Titanosaurus madagascariensis Depéret (1896), is a species founded on scanty material which includes a humerus, two caudal vertebrae, and a large dermal ossification, which probably was the base of a sharp conical spike, as in *Saltasaurus loricatus*. According to a reinterpretation by Huene (1929a) this scute does not pertain to this form or to any series of dermal bone. The result of the studies of the specimens of *Saltasaurus*

loricatus and the reinterpretations of similar elements like the dermal ossifications of titanosaurids (Powell 1980 and this work), shows that the original interpretation of Depéret was correct and that *Titanosaurus madagascariensis* is therefore referred here to the subfamily titanosaurinae.

C. ASIA

1. India

Given the palaeontological and palaeogeographical significance of the specimens listed from India, it is unfortunate that the work has been based in large part on isolated specimens, many of which are badly preserved and incomplete. There is more available material for analysing the geologic antecedents and characteristics known from the South American localities.

The oldest descriptions of specimens pertaining to the family Titanosauridae were of fossils found on the Indian peninsula. The first references were made in 1862, when Falconer described two caudal vertebrae with recognised reptilian affinities, without giving a formal name. The notes were published after his death as part of his palaeontological memoirs.

Hislop (1864) referred to discoveries in the Pisdura locality. Among the figured material were vertebrae and a femur which surely belongs to a titanosaurid. Although the specimens have disappeared (Pascoe 1963 or 1964), these data were used later to obtain additional fossil specimens.

Falconer's specimens were restudied by Lydekker (1877). From later comparisons it was deduced that the vertebrae in question belonged to the caudal region of a dinosaur. Based on these specimens he proposed a new genus and species: *Titanosaurus indicus*. An incomplete femur, found by Medlicott in 1871, came from the same area, but from a different stratigraphic level (Huene & Matley 1933). It is described in the same work by Lydekker (1877) and designated there as a 'cotype', because it was thought to be taken from the same 'Formation'. This specimen, very incomplete, without the articular ends and exposed only on the anterior face, has no usable diagnostic characters.

Lydekker (1879) redescribed *Titanosaurus indicus*, reproducing the illustrations of Falconer (1868), and also described a new species based on caudal vertebrae, *Titanosaurus blandfordi*, from levels of the Lameta Group near the Pisdura area.

Huene and Matley (1933) made a broad study of the Indian saurischians and ornithischians, revising the previously described specimens, and describing new ones. Among that latter was a fragment of a skull of a sauropod which was interpreted as a new species: *Antarctosaurus septentrionalis*. To this new species were also assigned various isolated specimens, among them a caudal vertebra.

Recently, Berman and Jain (1982) described a cranial roof of a sauropod, surely a titanosaurid. In the same paper is included a revision of the specimens which came from the Late Cretaceous fossil localities.

The major part of the formations in India are localised in the central area coming from the Lameta Group. This entity is lithologically composed of light colored limestone, sandstone and clays, and has a thickness varying between 6 m and 30 m (Chatterjee 1978). The Lameta Group rests unconformably upon the Jabalpur Group, composed of Cambrian metamorphics (Chatterjee 1978) and is covered by the 'Deccan Traps' a group of basalts which make the grand 'plateau' (Pascoe 1963 or 1964). Chanda and Battacharya (1966) recognised three formations in the Lameta Group: Greensand below, Limestone in the middle and for cover, the Sandy Limestone.

a. Bara Simla, Jabalpur

This fossil locality is situated on the western slope of Bara Simla Hill near Madhya Pradesh. The remains of tetrapods were discovered at two different levels at this locality. The oldest was at the top of the Greensand Formation, (Chatterjee 1978). It is known as the 'Carnosaur bed'. Here a good number of carnosaur bones were found, besides sauropods and coelurosaurs.

The Greensand Formation is composed of greensands, and occasionally other colours which vary in a very wide range, it is friable and has some rounded quartz. The date of the fossiliferous level is not available, as it seems to be a different facies. The age assigned to this fossiliferous level has been estimated as Turonian by Huene and Matley (1933), and Robinson (1967), while Chatterjee (1978) considered it to be Santonian or earlier, on the basis of a reinterpretation of the material described by Huene and Matley (1933), and reinterpreting one of the species of carnosaur to belong to the Family Titanosauridae, known from the end of the Late Cretaceous.

The higher fossiliferous unit at Bara Simla is at the base of the Sandy Limestone Formation and is known as the 'Sauropod bed'. From this unit came the vertebrae of *Titanosaurus indicus* described by Lydekker (1877), not the former used as a cotype (Huene & Matley 1933). From here also came a series of specimens collected by Matley, which also pertained to the sauropods described by Huene and Matley (1933). Among these in the basin were a pair of vertebrae that may correspond to the same individual as the vertebrae described by Lydekker (1877) and the specimens described as *Antarctosaurus septentrionalis* Huene and Matley. In the opinion of Matley (1929) cited in Berman and Jain (1982), this unit is composed of red and green clays. The estimation of the age of this unit coincides with similar estimates much earlier for the 'Carnosaur bed'.

b. Chota Simla, Jabalpur

This formation is located on the slopes of Chota Simla Hill, close to Jabalpur, and was explored by Matley

between 1932 and 1933, with the result that he obtained excellent specimens studied by Swinton (1947). In the opinion of this author, the principal fossiliferous horizon is located in the highest part of the Greensand Formation, a very little below the Limestone Formation, corresponding in time to the 'Carnosaur bed' mentioned at Bara Simla, located somewhat to the east of Chota Simla.

c. Pisdura Hill, Pisdura Basin

This locality is located 320 km to the south of Jabalpur. In the opinion of Berman and Jain (1982), the fossils come from a massive layer of red clays with occasional greenish interbeds, which lie just below the basalts known as the Deccan Traps.

This locality has produced the remains of *Titanosaurus blaudfordi*, cf. *T. indicus*, cf. *T. madagascariensis* and *Antarctosaurus* sp. (Huene & Matley 1933). There has also been cited the discovery of a turtle of the family Pelomedusidae: *Carteremys pisdurensis* based on a skull and plastron (Berman & Jain 1982).

The age of these units is interpreted by various authors with different results. Huene and Matley (1933) assigned it to the Turonian-Santonian, on the basis of a comparison at that time of the age of the rocks in Madagascar containing *T. madagascariensis*, that are now considered as Late Senonian. Robinson (1967) suggested Santonian age, but indicated that the presence of the mollusc *Bullius prinseprii* suggested a Maastrichtian age.

d. Dongargaon

This locality is situated somewhat to the west of Pisdura, and has provided fish and the remains of titanosaurs. Among them was found a cranial cap, mostly complete, and some vertebrae of titanosaurs and parts of turtle carapaces (Berman & Jain 1982). In the opinion of these authors, the remains of tetrapods mentioned above came from units of the green clays of the Lameta Group, assigned to a Santonian or Maastrichtian age.

D. EUROPE

1. Spain

The Spanish formations are located in the Cuenca de Tremp, Lérida and Cubilla, Soria (Sanz 1984). In Tremp, there are sites where bones assigned to *Hypselosaurus* sp. and the ornithischian *Rhabdodon priscum* (Sanz 1984) were found. The localities of Barranco de la Posa, near Isona; Barranco de Bastur; Oran; Orrit and Coll de Nargo have mainly eggs assigned to the Titanosaurid *Hypselosaurus* by Erben et al. (1979). According to these authors, the fossiliferous units correspond to the lower part of the lower 'Garumicense' sequence, for which is estimated an Early to Middle Maastrichtian age. In the opinion of Erben et al. (1979) the eggs located in this region were deposited close to the coastline of a bay in the banks and near the mouths and lesser courses of small rivers. The presence of marl containing small plates of gypsum is interpreted as an indication of the existence of temporary arid episodes, other deposits of lignite indicated abundant vegetation.

Lapparent and Aguirre (1956) cited in Steel (1970), have listed the genus *Titanosaurus* from the Cuenca de Trempe and Suterranda.

Sanz (1986) described osteoderms and a caudal vertebra of a titanosaurid from Armuña (Segovia). Material of crocodiles and turtles were also found at this site. The deposits are considered Campanian in age.

Laño, located in the Condado de Treviño (northcentral Spain) is a rich fossiliferous locality. A diversified vertebrate fauna is documented there: fishes (Lamniformes, Rajiformes, Lepisosteiformes), amphibians (Discoglossidae, Prosirenidea, Salamandridae), turtles (Dermatemyidae), lizards (Scincomorpha), snakes (Madtsoinae, Aniliidae), amphisbaenians, crocodiles, pterosaurs (Azharichidae), dinosaurs, and mammals (Theria) (Astibia et al. 1987, 1990). The dinosaurs are represented by theropod, ankylosaur, ornithomimid, and sauropod remains (Sanz 1986, Astibia et al. 1999). Some femoral material seems to be reminiscent of the abelisaurid theropods. Dromaeosaurid theropods could be represented by isolated teeth. This fossil site has yielded abundant sauropod titanosaur remains representing one of the better known European titanosaurid taxa described as *Lirainosaurus astibiae* Sanz et al. 1999. It is based on the following elements: a small occipital fragment, isolated teeth, dorsal and caudal vertebrae, a scapula, a coracoid, a sternal plate, several humeri, a fragment of ilium, a fragment of pubis, several femora, a tibia, a fibula, and several dermal scutes.

2. France

a. Area of Rognac and Velaux Provinces

The oldest citation concerning the remains assignable to the family Titanosauridae in France is Matheron (1869) and comes from discoveries in this area. The specimens in question come from a canyon close to Rognac. Velaux has produced eggs assigned to the family Titanosauridae, which have been studied by Van Straelen (1929). The fossiliferous units correspond to the Late Rognacian and Vitrolian (Maastrichtian)—(Ercen et al. 1979).

In this area remains of bones of the titanosaurid *Hypselosaurus priscus* Matheron 1869 and chelonians have been discovered.

b. Area of Rousset Province

This locality, situated to the east of Aix, is mentioned by Lapparent (1947), who indicates that bones and eggs collected there are assignable to the family Titanosauridae, now deposited in the Museo de Marsella. According to Lapparent (1947), these specimens come from the sands and clays of the 'Rognacian' (Maastrichtian).

c. Area of Fox—Amphoux, Province

The richness of this locality in quantity of specimens of vertebrates is commented on by Lapparent (1947). The

most interesting site is located 2 km to the east of Fox de Amphoux. The fossiliferous levels are discontinuous reddish and grey sandstone lenses of variable size within reddish lacustrine clays. Lapparent (1947) interprets these deposits as 'torrential deltas' flowing from a volcano into a lake.

That author indicates that this locality contains the titanosaurids *Hypselosaurus priscus* and *Titanosaurus indicus*, carnosaurs and an ornithomimid, *Rhabdon priscum* Matheron.

d. Saint Chinian Languedoc—Toussillon

This locality is mentioned by Lapparent (1947) and Lapparent and Lavocat (1955). The formation is located to the south of Saint Chinian, and is a deposit of red sandstones and clays assigned to the Maastrichtian. Lapparent (1947) lists for this locality the titanosaur *Hypselosaurus priscus*, and *Titanosaurus indicus* besides an indeterminate carnosaur and two ornithomimids: *Rhabdodon priscum* Matheron 1869, *Orthomerus transylvanicus* Nopsca 1915, and *Struthiosaurus ludgunensis* Nopsca, a supposed stegosaur [Editor's note: now considered to be an ankylosaur].

e. Campagne-sur-Aude (Département of l'Aude)

Rich fossiliferous deposits are exposed in this region. Fish remains (*Lepisosteus*), reptile (Chelonian indet., Crocodilia—Eosuchia, Theropoda, Sauropoda—Titanosauridae and Ornithomimida) were found in the Cretaceous sediments. Fossil invertebrates and plants are also present (Le Loeuff 1995). This area was previously discussed by Clottes and Raynaud (1982), Buffetaut et al. (1989), Le Loeuff (1991, 1992, 1995) and Le Loeuff et al. (1994). The fossiliferous level is included in the 'Marnes Rouges inférieures' Formation, (Marnes Rouges de la Maurine Member). This unit is considered Maastrichtian in age and is considered to have been formed under fluvial conditions; i.e. channels and flood plains deposits (Le Loeuff 1995).

From this area and at the site known as Bellevue-Site C3 of Campagne-sur-Aude (Clottes and Raynaud 1983; Buffetaut et al. 1989) the most important remains of French titanosaurids have been found. Le Loeuff (1995) described the armoured titanosaurid *Ampelosaurus atacis*. This taxon is based on teeth, dorsal and caudal vertebrae, ribs, hemapophyses, sternal plates, scapula, humerus, ulna, radius, pubis, ilium, ischium, femur, tibia, fibula, phalanges and dermal plates.

3. Rumania

The titanosaurids known from Rumania came from the localities of Valiora and Sinpetra (= Valiora and Szentpeterfalva) which are located in the Hatég Basin, Transylvania Province, formerly belonging to Hungary, thus figured in numerous publications and recently by Grigorescu (1983). In the opinion of this author, the specimens obtained from these localities were in the Sinpetra Strata which comprised sequences of sandstone, limonites and clays regarded as having been deposited in a system of anastomosing rivers.

The age of these deposits is considered to be Maastrichtian based on the fauna listed here.

The vertebrate fauna from these localities include chelonians, pterosaurs, crocodiles, carnosaurs, titanosaurs; iguanodonts, hadrosaurs and ankylosaurs. Among the titanosaurs Huene (1932) mentioned *Magyarosaurus dacus* Nopcsa 1915, *M. transylvanicus* Huene 1932 and *M. hungaricus* Huene 1932.

4. England

a. Isle of Wight

Lydekker (1888) published on a procoelus vertebra from the Wealden Formation, at Brook, Isle of Wight, England, which was interpreted as *Titanosaurus* sp. Huene (1929a) interpreted this form as a new species which he named *Titanosaurus valdensis*, considered a morphological intermediate between *T. indicus* and *T. blandfordi*. [Editor's note: *T. valdensis* is now *Luticosaurus valdensis* Le Loeuff (1993).]

If these specimens actually belong to the Titanosauridae, as the morphology of the caudal vertebrae indicate, this is at present the oldest known form of the family.

This is the point to consider, nevertheless, is this form related to the titanosaurs, or is it a distinct lineage which has the anterior portion of the tail with procoelus vertebrae, while the rest are amphicoelus or platycoelus? In this work it is not considered to belong to the Titanosauridae. The age of the Wealden Formation is estimated to be between the Late Berriasian and Barremian.

The highest levels correspond to the 'Upper Greensand', from which Lydekker (1888) cited other known vertebrae that in the opinion of Huene (1929a) are typically titanosaur, which he named *Titanosaurus lydekkeri*. This specimen came from the strata of Cenomanian age (Huene 1929a).

Finally, specimens considered as *Macrurosaurus semnus* Seeley discovered in Coldham Common, Barnell (Seeley 1876) in the 'Cambridge Upper Greensand' levels, are also assigned to the Cenomanian. Although various authors have included this form among the titanosaurs (Huene 1929a; Steel 1970; among others), in this work it is considered prudent not to include this form for the reason that although the anterior vertebrae are procoelus (which also occurs in *Tornieria* and also in *Dicraeosaurus*) the distal caudal vertebrae are amphiplatyan or amphicoelus. Furthermore, the vertebra illustrated by Seeley (1876) do not have the neural arch implaced on the anterior part of the centrum as is characteristic of the titanosaurs.

Acanthopholis platypus Seeley (1871) is based on some metacarpals, probably corresponding to *Macrurosaurus* according to Huene (1929a) and Steel (1970).

VIII. PALAEOGEOGRAPHIC IMPLICATIONS OF THE DISTRIBUTION OF THE TITANOSAURIDS

Continental vertebrates are restricted in their geographic distribution by marine and oceanic barriers, which affect all forms, except the birds (Hallam 1973).

Occasionally these barriers break totally or partially and the faunas disperse outside the area of original distribution in diverse forms.

The bridges, 'land bridges' or 'corridors', allow the free circulation of faunas in both directions.

There also exists 'filter bridges', which are similar to those mentioned above, with the difference that climatic or other factors exist which filter or permit the passage of some selected forms. The 'sweepstake routes' permit migration to cross marine barriers, by the medium of 'natural raft' (Simpson 1940).

The titanosaur dinosaurs, with their great bulk, have the most limited possibilities compared to small vertebrates such as turtles, lizards, snakes, amphibians and small mammals, as they could not have dispersed by natural rafts, which means they must have travelled by bridges.

With the advent and acceptance of the theory of continental drift, other mechanisms which would explain the distribution of faunas were supplement with one called 'Noah's Ark' (McKenna 1973), which assumes that a displaced continental mass carries with it a fauna 'cargo' from the larger landmass it broke away from.

The titanosaurs, found in the Cretaceous of distinct regions, some of these widely separated today, permit the establishment of a series of interesting palaeobiogeographic conclusions which confirm those obtained on the basis of other fossil groups for the interpretation of the areas where the data provided by other taxonomic groups is limited. The palaeobiogeographic utility is limited to what is now known of the family which is particularly diversified in the Senonian of the Gondwana continents (South America, India, Madagascar and Africa). When more is known of its distribution in Laurasia, it will make the sauropods a trustworthy element for postulating uniting of the continents where they are found.

It is necessary, nevertheless, to stress some limited interpretations derived from the characteristics of the specimens which constitute the Titanosauridae and the taphonomic processes which have affected them.

Most of the titanosaurid specimens, as pointed out in other parts of this work, were preserved in fluvial sediments, which led to the break up of the skeletons of these great reptiles. This has led to errors or confusion, as in the case of *Titanosaurus indicus* and *Neuquensaurus* (= '*Titanosaurus*') *australis*. The second was interpreted

erroneously by Lydekker (1893) and Huene (1929a) as pertaining to the genus *Titanosaurus*, which for a long time was a classical example of the disjunct distribution of a genus of continental vertebrates (e.g. Huene 1929a; Hallam 1973; Cox 1974; Colbert 1952).

Finally, imperfections of the fossil record means that the absence of a taxon on a continent does not absolutely prove its former absence as a living animal.

Here it is pointed out that, sometimes the palaeontological information has not been used with the necessary care. We know of cases in which data and fundamental concepts were incorrectly stated, as for example Axelrod (1975, p. 76), when analyzing the paleoposition of India and the palaeontological evidence relating to this problem said: '... India has Late Cretaceous sauropod dinosaurs (*Laplatasaurus*, *Antarctosaurus*, *Titanosaurus*) that are recorded from other regions, notably Argentina, Europe, Africa and Australia'. The presence of titanosaurs on this last continent has not been documented or previously reported.

A. South America and North America in the Late Cretaceous

The presence of *Alamosaurus sanjuanensis*, the only representative of the family Titanosauridae whose presence is known in North America, suggests that this continent and South America were very close at the end of the Late Cretaceous, allowing the passage of the titanosaurs by a land bridge (Bonaparte 1984a, b and c) or less likely by a long island arc (Casamiquela 1980; Cox 1980).

This hypothesis is consistent with the evidence provided by other groups of vertebrates and even plants, both fossil and living, as has been suggested by Simpson (1951), Etheridge (1959), Casamiquela (1964, 1980), Langston (1965), Savage (1966, 1982), Reig (1968), Sloan (1970), Sigé (1971), Hoffstetter (1976), Rage (1978, 1981), Brett-Surman (1979), Hallam (1981) and Bonaparte (1984a, b), having been amplified in treatises by Bonaparte (1984b, c).

The Hadrosauridae (ornithischian dinosaurs), constitute the primary evidence in favor of the hypothesis of this union. They are found in the Late Cretaceous of Río Negro Province (Casamiquela 1964) and Chubut (Brett-Surman 1979), and ichnites in the province of Salta (Alonso 1980). There are now new specimens in the Campanian-Maastrichtian in two localities in Río Negro Province: Estancia Los Alamitos (Bonaparte 1984a, b; Sepúlveda et al. (in press)) and Salitral Moreno, a new locality mentioned in this work.

This family dispersed into South America from North America in the Late Cretaceous (Casamiquela 1980; Brett-Surman 1979; Hallam 1981), probably in the Campanian (Bonaparte 1984a, b, c), surely utilizing the same route as the titanosaurs.

The specimens of 'Los Alamitos' have been identified as *Kritosaurus*, a taxon which is found in the Campanian of North America (Bonaparte 1984a). This has made possible great precision in the dating of the connection and brought additional support for the hypothesis of the existence of the terrestrial bridge between North and South America in the last quarter of the Late Cretaceous.

The ceratopsians are pointed out with other groups of immigrant reptiles in the Late Cretaceous of South America (Bonaparte 1984b, c), and is based on the specimen of *Notoceratops bonarellii* described by Tapia (1919) and re-studied by Huene (1929a). Although the presence of this group should not be disregarded, the possibility must be pointed out that the specimen illustrated could belong to a hadrosaur, a group known in the area.

As pointed out by Rage (1978), the boid snakes had apparently a Gondwana origin and seem to have invaded North America contemporaneously with the interchange of the dinosaurs which has been documented in the Campanian of New Mexico and Canada, and more so in the latest Cretaceous.

Among the lizards, the dispersal travelled the same route in the Late Cretaceous as was used by the hadrosaurs, which are known in the Late Cretaceous of North America (Estes 1964, 1969), and the Early Tertiary of Brazil and north-west Argentina (Estes 1970; Bonaparte 1984b, c). The iguanids probably participated in this interchange, but in the opposite direction to the teiids; i.e. from South America to North America (Estes & Price 1973; Bonaparte 1984).

The crocodilians of the family Alligatoridae also participated in this exchange, invading from North America, where they are recorded in the Late Cretaceous. The oldest record in South America is Paleocene in age (Báez & Gasparini 1977).

The turtles of the family Pelomedusidae, also originated in Gondwana and are documented in the Late Cretaceous to Miocene of North America (de Broin 1980), suggesting a migration at the same time and the same direction as the titanosaurs (Bonaparte 1984b, c).

The marsupials appear in the Late Cretaceous of Peru (Sigé 1971) and much later in Bolivia suggesting, with the evidence from the Paleocene of Brazil, an early and important radiation of the Metatheria in South America favoring the hypothesis of South American origin or from other lands then connected (Antarctica-Australia) with a dispersal to North America (Marshall et al. 1983b). [Editor's note: There is now strong fossil evidence that marsupials were present both in North America and Asia much earlier in the Late Cretaceous than they were in South America; e.g. Rougier et al. (1998).]

Marshall et al. (1983a) consider that the notoungulates had dispersed into South America from North America surely in the Late Cretaceous.

The study of the marine bivalves of the Cretaceous indicate endemicity during the Coniacian to Maastrichtian, which is consequently interpreted as owing to the isolation of the Caribbean from the Pacific (Kauffman 1973), partially or totally, for a short period of time.

Bussing (1976) has made a revision of the distribution of the living freshwater fish, suggesting a dispersion during the Late Cretaceous-Early Tertiary between the two Americas.

The studies of the distribution of the herpetologic fauna of the American continents, with special reference to Central America, indicates equally a continuous geography and similar tropical reptile fauna at the end of the Cretaceous and the beginning of the Tertiary in the three Americas, (Savage 1982).

Although the palaeontological evidence and the analysis of the distribution of some vertebrates concurs in indicating the existence of an island chain between South America and North America at the end of the Late Cretaceous, the geophysical and geologic studies made in the Caribbean area point out a series of interruptions between them, which results in a picture incompatible with the palaeontological evidence outlined above.

There are a series of palaeogeographic reconstructions concerning the relative position of both continents in the Cretaceous. Dietz and Holden (1970) and Irving (1977), indicated North and South America were certainly widely separated. While others, as Smith et al. (1973), and Freland and Dietz (1971) located the two continents as certainly very close, with Central America united as a peninsula to North America.

On the other hand, there are other points of view concerning the palaeogeographic and zoogeographic evidences. According to McKenna (1981), and on the basis of the study of Ladd (1976), the two Americas seem to have stayed very close together during the period of time between 80 and 56 million years.

Dengo (1975), and Lillegraven et al. (1979), indicated the presence of a volcanic chain which connected Central America with Ecuador and which probably existed in the Campanian (Complex of Nicoya). It was probably a 'rosary' of volcanic islands which could have served as a limited dispersal route ('stepping stones', Simpson 1940), and which could transform into a connection, corridor or land bridge in some of the Late Cretaceous regressions, probably in the Campanian (Harrington 1968) probably associated with a large tectonic event which affected all of Central America in the Campanian (Aubouin et al. 1981).

Schmidt-Effing (1979) has indicated agreement with the existence of emerging land in the Panama region in the Campanian-Maastrichtian.

In summary, it should be said in spite of some palaeogeographic reconstructions of the Americas in the Late Cretaceous that indicate separations between them, there exists much palaeontological evidence among which is included the presence of the Titanosauridae, indicating that the two continents continued to be connected, probably across Central America, in concordance with recent geological studies of Central America and north-western South America.

B. Africa and South America during Late Cretaceous

The list of titanosaurs in Africa is scanty, characterised by isolated specimens, generally caudals and other specimens more complete but little studied.

The formations are concentrated in the Central Sahara (Niger and Sudan) and the Eastern Sahara (Stromer 1932; Lapparent 1960; de Broin et al. 1974 and Taquet 1977).

The age assigned to the sediments with these remains is older than the figure best known for South America: they are designated in Africa as Aptian.

The presence of closely related titanosaurs in South America, Madagascar and India, indicates in the African Late Cretaceous that there were titanosaurs as in South America.

The evidence provided by the fossil vertebrates indicates that Africa and South America maintained land connections for at least the Aptian, with the presence of Uruguayan crocodiles of the genus *Araripesuchus* in Brazil and Niger (Buffetant & Taquet 1979), as well as pholidosaurid crocodiles of the genus *Sarcosuchus* inhabiting a lake environment (Gasparini 1981).

Also, the pleurodire turtles of the family Araripemidae are found in the top of the Aptian of Niger and Brazil (de Broin 1980), reinforcing the evidence pointed out above of the union of both continents in the Aptian.

The separation between the South American and African continents is among the best documented geologic events. The beginning of the fragmentation occurred with an axis of expansion in the Early Cretaceous, at 127 million years ago. And in the Aptian, the marine waters partially invaded the graben, accumulating deposits of evaporates in the area then located close to the coasts of Brazil and Africa (Windley 1977).

Reyment (1969), deduced from the evidence provided by the ammonites that during the Albian (106 million years b.p.), Cenomanian (100 million years b.p.), and Turonian (94 million years b.p.), there occurred a series of transgressions and regressions, with a definite separation in the Turonian (Reyment & Tait 1972).

Nevertheless, the similarity pointed out between the titanosaurs of the Late Cretaceous of India and Madagascar with those of South America, suggests the

possibility of the tie between Africa and South America in the Late Cretaceous, probably in the Senonian. This hypothesis concurs with the assertion by Rage (1981) explaining the presence of the pipid frog *Xenopus* in the Early Senonian of Africa (de Broin et al. 1974), and in the Paleocene of Itaboraí, Brazil (Estes 1975a, b) and Laguna del Hunco, Argentina (Baez & Gasparini 1977).

Eventually the iguanids, although absent from the living African fauna are recorded there as fossils, must have emigrated to Africa and to Madagascar in the Late Cretaceous (Estes & Price 1973; Cracraft 1974), later becoming extinct in Africa, an episode which happened in the Late Cretaceous (Senonian). A joining of the evidence (palaentology and neontology) suggests that the frogs of the family Bufonidae had immigrated to Africa, participating in the last faunal interchange in the Mesozoic, occurring just before the division or, perhaps soon after it (Laurent 1979), which well could have occurred in the Late Cretaceous.

There is evidence which suggests inter-continental 'bridges' of greatest palaeobiological interest.

Some palaeogeographic reconstructions are accomplished on the basis of palaeomagnetic data, indicating that South America was very close to Africa in the area of the states of Ceara, Rio Grande do Norte and Paraíba in Brazil and the African areas of Sierra Leone, Liberia, Costa de Marfil and Ghana. It is very probable that during the regressive periods or those of active tectonic activity there existed the possibility of communication between both continents. Equally likely, this area coincided with the position of another important rise, the seismic rise of Ceara and Sierra Leone, which existed 80 million years b.p. (Kumar & Embley 1977), and either persisted or re-emerged in the Tertiary (Tarling 1982).

Other authors, such as Rage (1981) postulate a possible communication or bridge located much to the south, along the emergent Rio Grande and Walvis Ridges. Evidence exists that these rises represent 'marine mountains' in the process of subsidence, with this activity there were covering sediments containing fossils which are actually less deeply buried (Smith 1977). Probably a large island was formed, emerging for a length of 2–3 km above the sea during a long period between 75–85 million years b.p. (Thiede in Smith 1977; Tarling 1982).

Either of the two alternatives suggest 'filter' bridges, with few taxa participating in this exchange, and some taxa such as the pleurodire are seen as endemically precocious in the Late Cretaceous (de Broin 1980).

For example, consider the possibility of an established 'Walvis-Rio Grande Plateau' bridge with an African epicontinental sea. This constituted an insurmountable barrier during the Late Cretaceous, if one accepts as probable the hypothesis of Rage (1981) that the titanosaur

faunas and other vertebrates were found locally in the middle of the south-east region of Africa. The African epicontinental sea divided Africa in the Late Cretaceous, but according to the study of Reymont (1971) the tongues of the Mediterranean and Atlantic were united only temporarily in the Early Turonian and Early Maastrichtian. This permits consideration of the feasibility of a more simple route, between the area of Ceara, Rio Grande do Norte, Brazil and the region of Sierra Leone, Liberia, Marfil Coast and Ghana.

Whatever the actuality of passage and faunal interchange was between Africa and South America, it apparently permitted faunal elements to reach both parts of the African continent. In the north-west Africa extended to southern Europe and in its south-eastern part dispersal was possible in another direction to India and Madagascar. In synthesis, it could be said that the observed similarity between the titanosaurs of the Late Cretaceous of India, Madagascar and South America, suggests land ties with South America and Africa. These connections are supported by the available evidence of the distribution of the boids, of the frog genus *Xenopus* and later by the bufonids, coincident with the hypothetical passage of the iguanids in their route to Madagascar.

C. Africa and Madagascar during Late Cretaceous

The island of Madagascar has an interesting list of Triassic, Jurassic, and Cretaceous tetrapods in spite of its reduced territory if it is compared to the rest of Gondwana.

In the Late Cretaceous of Madagascar the titanosaurs, together with other vertebrates, have been recorded from the Majunga area. The palaeontological evidence clearly indicates that Africa and Madagascar had terrestrial connections during the Late Cretaceous, which very probably persisted until the Campanian.

The presence of *Titanosaurus madagascariensis* Depéret (1896) indicated connections with India and South America (via Africa). Nevertheless in the judgement of the author of the present work it is not certain that Depéret was correct in assigning the material available to him to the genus *Titanosaurus*. This matter could be decided with the study of additional specimens, such as those collected by Taquet (Russell et al. 1976).

Other evidence provided from the same formation of Majunga is *Trematochanpsa oblita* (Buffetaut & Taquet 1979), a terrestrial crocodile related to *Trematochanpsa taqueti* from the Early Senonian in Beceten, Niger.

The ties of Madagascar during the Late Cretaceous are also supported by the presence of '*Madisoia*' *madagariensis*, a genus listed in the Late Cretaceous of Niger. In the opinion of Rage (1978) it is tentatively of Gondwanan origin.

In the framework of the distribution of living reptiles, the presence of iguanas in Madagascar supports the

assumption that they existed in Africa (Estes & Price 1973) when they surely were also in South America. Here they are known, as has been said, since the Late Cretaceous (Cracraft 1974). This distribution is thus explained as not only the product of a dispersion concentrated in the Late Cretaceous.

There are, nevertheless, other alternatives which explain the presence of the iguanas in Madagascar, namely an entrance 'by raft' from Antarctica (Blanc 1983).

The pelomedusid turtles, present today in Madagascar, are probably a relic of those faunas distributed in the Late Cretaceous and Tertiary in the Gondwana areas (Báez & Gasparini 1977). The possibility of a dispersion happening in the Late Cretaceous of Madagascar was, eventually, supported by specimens of this age probably referable to the genus *Taphrosphys* (de Broin 1980).

Recently, Taquet (1982) analyzed new geologic observations consisting of the stratigraphy on the bottom of Mozambique Channel in relation to the palaeontological evidence of the Mesozoic and especially of the Late Cretaceous. The conclusion of the new work is that Madagascar was in the same position that it is now with respect to Africa from the Late Paleozoic, having an intermittent continental connection in the course of the Mesozoic, with a continental phase in the Late Cretaceous (Senonian), across an elevated area, The Davies (actually submerged). This follows on the basis of the discovery of continental sediments which underlie a sequence of limestones of Late Cretaceous–Pliocene age in this uplift, and this interpretation agrees with the observed endemism of the ammonites (Taquet 1982).

This uplift was brought about by upward movements in this area by the marine regression which Taquet (1982) located between the Cenomanian–Turonian and Maastrichtian transgressions.

D. India and Africa during Late Cretaceous

The resemblance of the Indian fauna with that of Madagascar and South America, shows the presence of at least one genus of titanosaurs, as indicated by Lydekker (1893), showing the possibility of a connection of the continental faunas of the Late Cretaceous of the Indian peninsula and the lands of the Southern Hemisphere.

Huene (1929a), although employing some erroneous identifications, developed a hypothesis which explained the disjunct distribution of this family and especially the genus *Titanosaurus* according to which the displacement limited a crossing by a corridor which hypothetically existed between South-east Asia and South America. This was made of bridges of solid earth and/or islands whose relics are New Guinea, Samoa, Tahiti and Tinian. This displacement happened, according to Huene (1929a), to South-east Asia principally in the Late Cretaceous, with the movement ending in the Late Cretaceous.

The acceptance of the dispersion and the ideas on the drift at present has allowed students of palaeobiogeography to understand the present distribution of plants and animals, and the palaeoflora and palaeofauna, without resorting to the complications and limited schemes based on filter bridges and excessively long corridors.

The presence of titanosaurs of the subfamily Titanosaurinae in India, documented in South America and Madagascar as the genus *Titanosaurus*, constitutes interesting evidence of the union of Africa, Madagascar with India in the Late Cretaceous.

This evidence is confirmed by the presence of the pelomedusid turtles in the Cretaceous at the Pisdura area (Berman & Jain 1982), and the union of the palaeofloras (Hallam 1981), which likewise suggest that Africa and the Indian Peninsula were connected in the Late Cretaceous.

This group of proofs illustrates in a clear manner that the Indian peninsula was not an 'island' navigating in the Indian Ocean during the Late Triassic as suggested in the reconstruction of Dietz and Holden (1970), or that the separation was concentrated in the Early Cretaceous as suggested by Irving (1977), except that it was sufficiently close to permit displacement until the Senonian.

Smith and Briden (1977) suggested that Africa, Madagascar, and India were connected until very late in the Cretaceous and even much later, and Sucs (1980), pointed out that the concept was supported by the titanosaurs.

The data provided by palaeontology is in accordance with the palaeomagnetic evidence which indicates the separation of the African continent and the Indian peninsula occurred in the course of time between the Late Cretaceous and the Early Tertiary (Valencio 1980).

Similar conclusions were obtained by McElhinny (1970), also based on palaeomagnetic data, that invoked a separation of India and Madagascar in the Late Cretaceous or much later in the Early Tertiary.

Smith and Hallam (1970), pointed out that the marine faunas indicated the existence of land barriers between the Indian peninsula and Africa–Madagascar until at least the end of the Cretaceous. Chatterjee (1984) made an analysis of the tetrapod faunas following the Mesozoic, which indicates that endemism did not exist, and indicated that India had been an island during millions of years in the lapse of time in this period. On the contrary, the Mesozoic and Tertiary vertebrates indicate it had narrow connections similar to that of Laurasia, suggesting that India was at no time far away from Asia. According to this same author, the Indian peninsula was originally situated between Somalia and Asia, and the Tethys Sea was narrow and intracontinental.

Part of this interpretation of the paleo-position of India agrees with the evidence which is pointed out in this work

and which suggests a late separation of India and Madagascar, Africa, and a rapid connection in the Early Tertiary with Asia (Sahni et al. 1982). Nevertheless, the faunistic resemblance between India and North America pointed out by Chatterje (op. cit.) for this is mistakenly obtained from a misleading methodical procedure, in which fragmentary Indian specimens have been referred to well known taxa of the Northern Hemisphere (e.g. Ankylosauridae, Tyrannosauridae, Allosauridae, Ornithomimidae), although in other cases does not consider the possible centres of origin of each group (e.g. Titanosauridae) nor the known time of its dispersion. In this manner there is a maximum coefficient of similarity between the North American terrestrial tetrapods and the Indian.

In agreement with the evidence presented in this work, it appears that this interpretation is mistaken, in the faunal and floral relations with Madagascar, Africa and South America. It is admitted nevertheless, there is the possibility of a narrow Tethys Sea and a connection with Asia, temporarily in the Early Tertiary.

E. Africa and Europe during Late Cretaceous

The presence of titanosaurs which could be included in the subfamily Titanosaurinae in the Late Cretaceous (Maastrichtian) in Spain, France and Rumania, presumes the existence of some type of corridor to cross the emergent areas at the end of the Late Cretaceous.

Other evidence of this connection is the discovery of mammals of the family Palaeoryetidae, of genuine Laurasian stock in the Paleocene of Morocco (Cappetta et al. 1978).

The turtles of the family Pelomedusidae, of Gondwana stock, are also listed in the Late Cretaceous and Oligocene of Europe (de Broin 1980) and are commonly found associated with the dinosaurs of the family Titanosauridae in the Late Cretaceous of South America. They are interpreted in this work as following the same migratory route to Africa and Europe.

Other taxa which have migrated along this bridge, are the sebecosuchian crocodiles. Forms assigned to this group are found in Germany (Langston 1975) and Portugal (Antunes 1975). Their presence has been interpreted as the product of two different routes: the first suggested by Buffetaut (1980) and Rage (1981) who hypothesise a migration from South America to North America and then to Europe. The second, proposed much later, and based on the discovery of ziphodont crocodiles in the Eocene of Algeria is considered as valid evidence in favor of a migration from South America to Europe going through Africa (Buffetaut 1982). This route had been independently proposed by Bonaparte (1984) who dated it as Early Tertiary.

In this work it is suggested that there was probably a continental connection between Africa and Europe in the Late Cretaceous, (Campanian?, Maastrichtian) used by

the titanosaurs, the pelomedusid turtles, probably the crocodiles related to the Trematochampsidae (Buffetaut 1980) and the caracid fish from Africa to Europe. The palaeoryetid mammals had moved in the reverse direction.

The sebecid crocodiles, the ceratophryinae anurids and the didelphids migrated at the same time or much later, as suggested by Bonaparte (1984b), without definite existing arguments in favor of any of these hypotheses.

Among the ornithischians, is the extinction of the psittacosaurids and, among the multituberculates the plagiaulacoids disappeared.

In the marine environment there is the extinction of the Stenopterygiidae and Ophthalmosauria (Ichthyopterygia) and Plesiosauridae (Sauropterygia) (Appleby et al. 1967).

The radiation of the angiosperms in the Cretaceous coincides with the appearance of the hadrosaurs in Laurasia and the titanosaurs in the continents which formed part of Gondwana. Both dinosaur groups being primary consumers. Krassilov (1981) recognised that the replacement of the dinosaur fauna at the end of the Late Cretaceous is clearly tied to the change of vegetation of the whole world, as also inferred by Bonaparte (ms). In South America, this change was documented although its data is not complete (Archangelsky 1970).

At this moment there are limited beds with dates based on megafossils containing plants in the Late Cretaceous of South America.

Although it is common to discover fossil tree trunks associated with the remains of titanosaurs, there are few studies of these plant specimens. The contribution of Torres and Rallo (1981) should be mentioned here where they described a combination of forms from the Pichasca, Chile locality.

There are equally few studies of the Cretaceous flora based on the megaflora (Romero & Arguijo 1981). These authors outlined a panorama of the flora of southern South America in the Late Cretaceous, pointing out the following palaeoecological and evolutionary connections between the titanosaurs and plants.

The flora of the Late Cretaceous is new, none of the known forms are from the Early Cretaceous. Furthermore, there is a strong turnover again going into the Tertiary, because only 8 of the 46 Cretaceous species carry through into the Tertiary.

Of the 46 Late Cretaceous plant species known, 6 are pteridophytes, 5 gymnosperms, none are monocotyledons and 35 dicotyledons.

Of this group, the angiosperms are mostly represented by Magnoliaceae (14 species), Dilleniaceae (7 species), Rosiaceae (6 species) and Hamameliaceae (3 species).

As has been shown above, the advent of the Late Cretaceous had a different development in Gondwana, and especially South America, with respect to dinosaurs.

Examination of the fossil records indicates that at the end of the Early Cretaceous, the best adapted and potentially adaptable family of sauropods was the Titanosauridae. They flourished in the Late Cretaceous and survived after all the other sauropods had become extinct. After the separation from Africa, the isolation of the titanosaurs in South America during much of the Late Cretaceous, without competition from other herbivorous dinosaurs, resulted in a modest diversification of the family into, at most, four subfamilies with a total of less than 8 genera.

The armoured condition of various forms of titanosaurs on the other hand, shows that they did undergo significant evolutionary change during the Late Cretaceous. The armour occurs as a diversity of large, morphologically diverse dermal plates with spikes, and in the case of *Saltasaurus loricatus*, as interdermal ossicles.

At the end of the Cretaceous, during the Campanian–Maastrichtian (Casamiquela 1980; Bonaparte 1984a, b; Bonaparte et al. 1984), a land connection was established which permitted the dispersion of the titanosaurs to North America, where until now only *Alamosaurus sanjuanensis* has been discovered (Gilmore 1921; 1946; Mateer 1976; Kues et al. 1980).

As a product of this connection, the hadrosaurs and other groups of terrestrial vertebrates penetrated South America, upsetting the equilibrium which had developed during the long isolation of the Early Cretaceous.

The discoveries recently found at Irgeniero Jacobacci (Casamiquela 1980), Estancia Los Alamitos (Bonaparte et al. 1984) and Salitral Moreno (Powell 1987) indicate associations of hadrosaurs and titanosaurs. In the first two, the remains of titanosaurs are very scanty in relation to the hadrosaurs. In the third locality, the results of the preliminary work indicate that both groups are abundant.

IX. PHYLOGENETIC APPENDIX

The Cretaceous sauropod fossil record increased markedly after the writing of the Ph.D. dissertation (Powell 1986) which constitutes the core of this contribution. Consequently many more aspects of the titanosaurid anatomy are presently known. Non-titanosaurid Cretaceous sauropods have also been found, some of them probably related to the origin of titanosaurs. Sauropod phylogenetic studies have been presented by several authors have allowed serious phylogenetic analysis such as those of Upchurch (1994; 1995), Salgado et al. (1997), Wilson & Sereno (1998), and Sanz et al. (1999). In the latter, character analysis of several poorly known titanosaurids are included, as those of *Epachthosaurus sciutoi*, based on an articulated specimen, and the Spanish *Lirainosaurus astibiae*. The

present analysis considers most of the characters used by Sanz et al. (1999). The following taxa has been added: *Titanosaurus colberti* from India (Jain & Bandyopadhyay 1997), *Alamosaurus sanjuanensis* from United States (Gilmore 1922; 1946), *Ampelosaurus ataxis* from southern France (Le Loeuff 1995) and *Aeolosaurus rionegrinus* from Patagonia (Powell 1986; 1987a)

X. CHARACTER ANALYSIS

- 1) Tooth morphology (Spatulate 0 - Peg-like 1)
Most authors have considered two main tooth morphotypes within sauropods. It seems evident that the spatulate morphotype (camarasaur-like) can be considered as primitive. They are present both in 'cetiosaurs' and in more derived sauropods, including camarasaur and brachiosaurs. The other sauropod tooth morphotype is characterised by a subcircular cross section of the crown (diplodocid-like), which is considered as derived.
- 2) Infraprezygapophysial lamina in first dorsals (Single 0 - Double 1).
This is an autapomorphic trait for *Saltasaurus loricatus*, where the prezygapophysis is reinforced by means of two thick laminae (Powell 1992).
- 3) Axial keel in the centrum of dorsal vertebrae (Absent 0 - Present 1).
- 4) Pleurocoelic cavity in medial and posterior dorsal vertebrae (Poorly developed 0 - Poorly developed but with clearly defined outline 1 - Developed and clearly defined 2).

The main difference between the primitive and the two derived character states is the presence in the derived ones of a well-defined pleurocoelous outline that clearly marks the margin of this structure.

- 5) Horizontal surface at the end of diapophyses in the posterior dorsal vertebrae (Absent 0 - Present 1).

This character state is clearly observed in several genera, as *Lirainosaurus*, *Saltasaurus*, *Epachthosaurus*, and the Peirópolis titanosaur. This feature is independent from the diapophysis position, i.e. it appears in forms with both erect and laterally directed diapophyses. This trait seems to be related with the existence of ossified tendons that would have axially joined the diapophysial dorsal surfaces. In fact, in the Peirópolis titanosaur there is actual evidence of these ossified tendons. In *Lirainosaurus*, a sagittal groove is developed in that flat surface, probably related to those elements.

- 6) Hyposphene-hypantrum articulation in posterior dorsals (Present 0 - Absent 1).
The derived condition, absence of hyposphene-hypantrum articulation, is present in most of the known titanosaur genera. It can be observed in some recently described genera like *Epachthosaurus* (Powell 1990) or *Andesaurus* (Calvo & Bonaparte 1991). Bonaparte and Coria (1993) have proposed an independent derived character state in

Argentinosaurus (hyposphene-hypantrum hypertrophied). Nevertheless, a new interpretation is suggested herein: *Argentinosaurus* actually lacks a true hyposphene. A functionally similar structure is developed by reinforced infra-postzygapophysial laminae.

- 7) Opisthocoely in posterior dorsal vertebrae (Absent 0 - Slightly developed 1 - Developed 2). Dorsal vertebrae with amphiplatyan centra is the primitive character state. A clear trend of developing opisthocoelous presacral vertebrae towards the sacrum can be observed within the Sauropoda. A developed opisthocoely in the posterior dorsal vertebrae could be related to an increased ability to prevent dislocation.
- 8) Postzygodiapophysial lamina in posterior dorsal vertebrae (Absent 0 - Present 1).
- 9) Spinodiapophysial lamina in posterior dorsal vertebrae (Absent or incipient 0 - Present 1).
- 10) Aliform process of the neurapophyses on mid dorsal vertebrae (Absent 0 - Present 1). This character is defined as a triangular flat expansion laterally attached to the neural spine just above the postzygapophyses.
- 11) Pleurocoelous outline in anterior and mid dorsal vertebrae (Rounded posterior margin 0 - Acuminate 1)
- 12) Spino-diapophysial accessory lamina in posterior dorsal vertebrae (Absent 0 - Present 1)
- 13) Neurapophyses in dorsal vertebrae (High 0 - Low 1; Fig. 1).
- 14) Prespinal lamina on mid and posterior dorsal vertebrae (Absent 0 - Present with poorly developed basal branching 1 - Branching well developed 2.)
- 15) Osseous tissue of axial skeleton (Not cancellous 0 - Cancellous in presacral vertebrae 1 - Cancellous in presacral and in anterior caudal vertebrae 2).

This type of osseous tissue can be present not only in the axial skeleton, but also in ilium and ribs (*Saltasaurus*, *Epachthosaurus*). Many non-titanosaur sauropods lack this cancellous condition (diplodocids, camarasaurids, etc.). Nevertheless, some of them present a similar feature (Huene 1929a; Longman 1933; Salgado 1993).

- 16) Position of the articular surface of prezygapophysis and postzygapophysis in anterior caudal vertebrae (Sloped 0 - Subhorizontal 1).
- 17) Developed posterior condyle in anterior caudal vertebrae (Absent 0 - Present 1). Most authors describe this feature as presence/absence of procoelous caudal centra, being traditionally one of the most significant traits in the diagnosis of titanosaurs (Lydekker 1893; Huene 1929a; Powell 1986; McIntosh 1990). The procoelous condition has been considered sufficiently significant to form the basis for including several forms like *Tornieria* (McIntosh 1990), *Malawisaurus* (Jacobs et al. 1993) and an undetermined sauropod from the Patagonian Cretaceous (Salgado 1993) within the titanosaurs.

Since several forms such as *Andesaurus* have procoely (*contra* Calvo & Bonaparte 1991) but lack a developed posterior condyle, this structure has been chosen as a more reliable feature.

- 18) Neurapophyses in anterior caudal vertebrae (Laterally compressed 0 - Laterally expanded 1). The first character state means that the transverse neurapophysial width is greater than the anteroposterior dimension.
- 19) Restricted articular condyle in posterior caudal vertebrae (Absent 0 - Present 1). This feature is unknown in non-titanosaur sauropods. It is present as a convergence in other archosaurs, like eusuchian crocodyles (AD Buscalioni, pers. comm.).
- 20) Condylar groove in the posterior articular surface of distal caudal vertebrae (Absent 0 - Sagittal 1 - U-shaped 2). The condylar groove may be associated with the occurrence of an intercentral ligament, which would reinforce the distal part of the tail.
- 21) Depression under the prezygapophyses in anterior caudal vertebrae (Absent 0 - Present 1).
- 22) Lamina in the interzygapophysial fossa in anterior caudal vertebrae (Absent 0 - Present 1; Fig. 1).
- 23) Prespinal and postspinal laminae in anterior caudal vertebrae (Incipient 0 - Developed 1)
- 24) Relative dimension of the posterior articular surface of mid caudals (Dorsoventral dimension greater than or similar to transversal dimension 0 - Smaller 1)
- 25) Hemapophysial ridges in mid caudal vertebrae (Absent 0 - Present 1; Fig. 1)
- 26) Axial ventral crest placed between the hemapophysial ridges of mid caudal centra. (Absent 0 - Present 1; Fig. 1).
- 27) Spino-postzygapophysial structure in posterior caudal vertebrae (Posteriorly projected 0 - Non projected 1; Fig. 1).
- 28) Lateroanterior process on sternal plate (Absent 0 - Present 1; Fig. 2).
- 29) Anteroventral ridge of sternal plate (Absent 0 - Present 1; Fig. 2)
- 30) Medial prominence close to the dorsal margin of the scapular blade (Absent 0 - Present 1; Fig. 2).
- 31) Ridge on the ventral margin of the medial side of scapular blade (Absent 0 - Present 1; Fig. 2).
- 32) Anteromedial coracoid outline (Rounded 0 - Straight 1). The general outline of the coracoid has been defined as subquadrangular by several authors (Huene 1929a, Powell 1992; McIntosh 1990). Nevertheless, I think that this character is better described by using only the anteromedial part of the coracoid outline.
- 33) Position of coracoidal foramen (Close to scapular margin, relatively far from dorsal margin 0 - Far from scapular margin 1 - Close to scapular margin and close to dorsal margin 2).
- 34) Deltopectoral crest of humerus developed and medially twisted (Absent 0 - Present 1)

A poorly developed deltopectoral crest is present in 'cetiosaurid' genera as *Patagosaurus* and *Omeisaurus* (He et al. 1984).

- 35) Posterior supracondylar ridges on the humerus (Incipient 0 - Prominent 1)
- 36) Depression at base of pubic peduncle of the ilium (Absent 0 - Present 1).

- 37) Lateral expansions of ilium (Not expanded 0 - Anterolaterally expanded 1).

In the primitive character state, the preacetabular moiety of the iliac blade is relatively short. In *Haplocanthosaurus* an incipient laterally expanded blade is present, correlated with a slight increase in length of the preacetabular region. In the proposed derived character state, the anterolateral iliac expansion implies that the iliac blade twists to reach a gently sloped disposition. Thus, the distal anterolateral iliac surface faces dorsolaterally.

- 38) Ischiatic process of ischium (Long and non-laminar 0 - Long and laminar 1 - Short and laminar 2).

- 39) Lateroproximal buttress of femur (Absent 0 - Present 1)

This structure is well developed in some genera such as *Saltasaurus* and *Argyrosaurus*, and can be observed in the femur described by Salgado and Coria (1993) associated with the Titanosauridae.

- 40) Fourth trochanter in femur (Prominent 0 - Reduced 1).

- 41) Angle between planes including the greatest proximal dimension of the tibia and that of the distal region (Low 0 - Almost perpendicular 1; Fig. 2).

- 42) Osteoderms (Absent 0 - Present 1).

Depéret (1896) was the first author who proposed the association between osteoderms and titanosaur remains, later suggested also by Bonaparte and Powell (1980), Powell (1980), Sues (1980), Sanz and Buscalioni (1987), Le Locuff et al. (1994) and Le Locuff (1995). Despite the fact that there is no direct evidence between specific titanosaur forms and the presence of a dermal skeleton, we consider reasonable that some genera such as *Saltasaurus*, *Lirinosaurus*, and *Ampelosaurus* were osteoderm-bearing sauropods. A well preserved articulated *Epachthosaurus* skeleton found at Ocho Hermanos (Chubut, Argentina) suggests that this primitive titanosaur lacked a dermal skeleton.

Discussion

The characters used in the matrix (Pl. 86) are similar to that published by Sanz et al. (1999). Just one character of the former matrix has been excluded. The following taxa have been added: *Titanosaurus colberti* (Jain & Bandyopadhyay 1997), *Alamosaurus sanjuanensis* (Gilmore 1946), *Ampelosaurus atacis* (Le Locuff 1995) and *Aeolosaurus rionegrinus* (Powell 1987b). *Patagosaurus* (Bonaparte 1986b) was chosen for out group comparison. Additional genera has been also considered as out group: *Volkheimeria* (Bonaparte, 1986b), *Omeisaurus* (He et al. 1984), and *Cetiosaurus* (Owen 1841). *Haplocanthosaurus priscus* (Hatcher 1903), *Andesaurus* (Bonaparte & Calvo 1991),

Opisthocoelicaudia (Borsuk-Bialynicka 1977), *Saltasaurus loricatus* (Bonaparte & Powell 1980), *Argyrosaurus* (Lydekker, 1893), *Epachthosaurus* (Powell 1990), a titanosaur from Peirópolis, Brazil (Powell 1987a), and the Laño sauropod form the ingroup. *Magyarosaurus* has been also considered (Huene 1932). These taxa, and other genera like *Antarctosaurus*, and *Neuquensaurus* have been finally excluded from the matrix because of the lack of information concerning many of the features analyzed herein.

One tree of 76 steps in length and a consistency index of 0.64 (Pl. 87).

Clade 1 (unnamed) is defined by the following synapomorphies: developed and clearly defined pleurocoelous cavity in medial and posterior dorsal vertebrae (4.2), slightly developed opisthocoelous in posterior dorsal vertebrae, reversed in *Argyrosaurus* (7.1), presence of spinodiapophyseal lamina in posterior dorsal vertebrae (9), acuminate pleurocoelic outline in anterior and mid dorsal vertebrae (11), poorly developed basal branching of the prespinal lamina on mid and posterior dorsal vertebrae, reversed in *Titanosaurus colberti* (14.1), hemapophyseal ridges in mid caudal vertebrae (25), straight anteromedial coracoid outline (32), and coracoidal foramen placed away from the scapulocoracoidal suture (33.1).

Clade 2 (Titanosauroida *sensu* Upchurch 1995) is defined by the following synapomorphies: prespinal and postspinal laminae in anterior caudal vertebrae (24) is another evolutionary novelty that characterises node 2 (reversed in *Saltasaurus*), ilium anterolaterally expanded (37), (character reversed in *Ampelosaurus*), presence of a lateroproximal buttress of the femur (39). Clade 2 is also characterised by a strongly developed opisthocoely in posterior dorsal vertebrae (7.2), reversed in *Argyrosaurus*, which displays weak opisthocoely (7.1).

Clade 3 (Titanosauria) is defined by the following synapomorphies: horizontal surface at end of diapophyses on posterior dorsal vertebrae (5) (parallel in *Haplocanthosaurus*), presence of developed posterior condyles in anterior caudal vertebrae (17), anteroventral ridge on sternal plate (29).

Clade 4 (Eutitanosauria) is defined by the following synapomorphies: absence of hyposphene-hypantrium articulations in posterior dorsal vertebrae (6), reduced fourth trochanter in femur (40), and the presence of osteoderms (43).

Clade 10 is characterised by an almost perpendicular angle between planes including the greatest proximal dimension of the tibia and that of the distal region (42).

Clade 5 is distinguished by the reversion of character 13, showing a high neuropophysis in dorsal vertebrae, and absence of the anteroventral ridge of sternal plate, which represents also a reversion.

Clade 7 is weakly supported by the reversion of character 24 to its primitive condition: incipient prespinal and postspinal laminae in anterior caudal vertebrae.

Clade 8 is characterised by a non-projected spinal postzygapophysial structure in posterior caudal vertebrae (27).

Clade 9 is characterised by the presence of an axial keel in the centrum of dorsal vertebrae, a parallel character in *Lirainosaurus*.

Ampelosaurus: distinguished by a laterally non-expanded ilia, which is a reversion of character 37.

Titanosaurus colbertii: distinguished by the absence of prespinal laminae on mid and posterior dorsal vertebrae (a reversion to the primitive character state: 14.0)

Lirainosaurus: distinguished by a sagittal condylar groove in the posterior articular surface of distal caudal vertebrae (20.1), a depression under the prezygapophysis in anterior caudal vertebrae (21) and a coracoidal foramen close to the scapular and dorsal margins (33.2).

Epachthosaurus: distinguished by U-shaped condylar grooves in the posterior articular surfaces of distal caudal vertebrae (20.2), and well developed branching of the prespinal laminae on mid and posterior dorsal vertebrae (14.2). This latter character is also present in parallel in *Andesaurus*. Presence of a depression under the prezygapophysis in anterior caudal vertebrae (21) is also a parallelism in *Lirainosaurus*.

Argyrosaurus: distinguished by a slightly developed opisthocoely in posterior dorsal vertebrae, a reversed character (7.1)

Saltasaurus: distinguished by double infraprezygapophysial laminae in first dorsals (2), cancellous osseous tissue in presacral and anterior caudal vertebrae (16.2), incipient prespinal and postspinal laminae in anterior caudal vertebrae (23.0), and presence of axial ventral crest placed between the hemapophysial ridges of mid caudal centra (26).

Andesaurus: distinguished by a well developed prespinal lamina, branching on mid and posterior dorsal vertebrae, independently acquired in *Epachthosaurus*.

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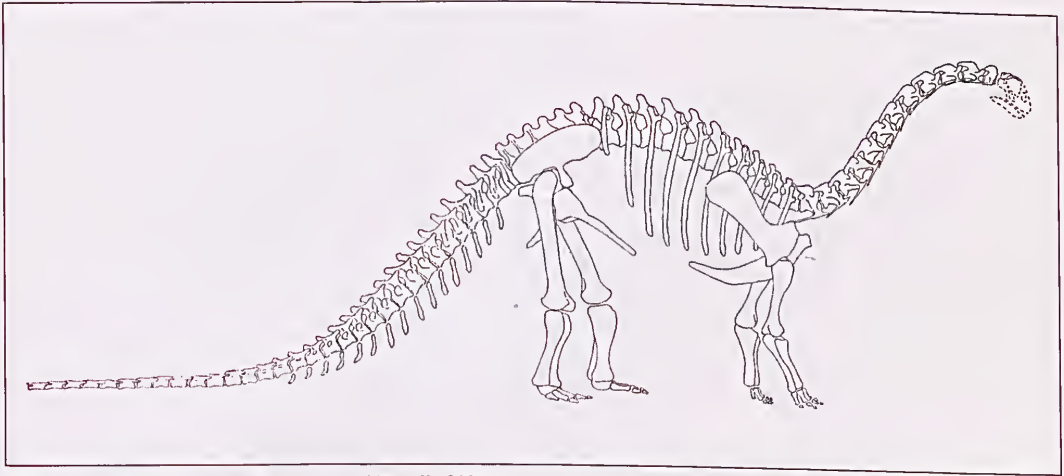


Plate 1. *Saltasaurus loricatus* Bonaparte and Powell 1980. Reconstruction of the skeleton based on disarticulated bones of different individuals from the El Brete locality, Salta Province, Argentina.

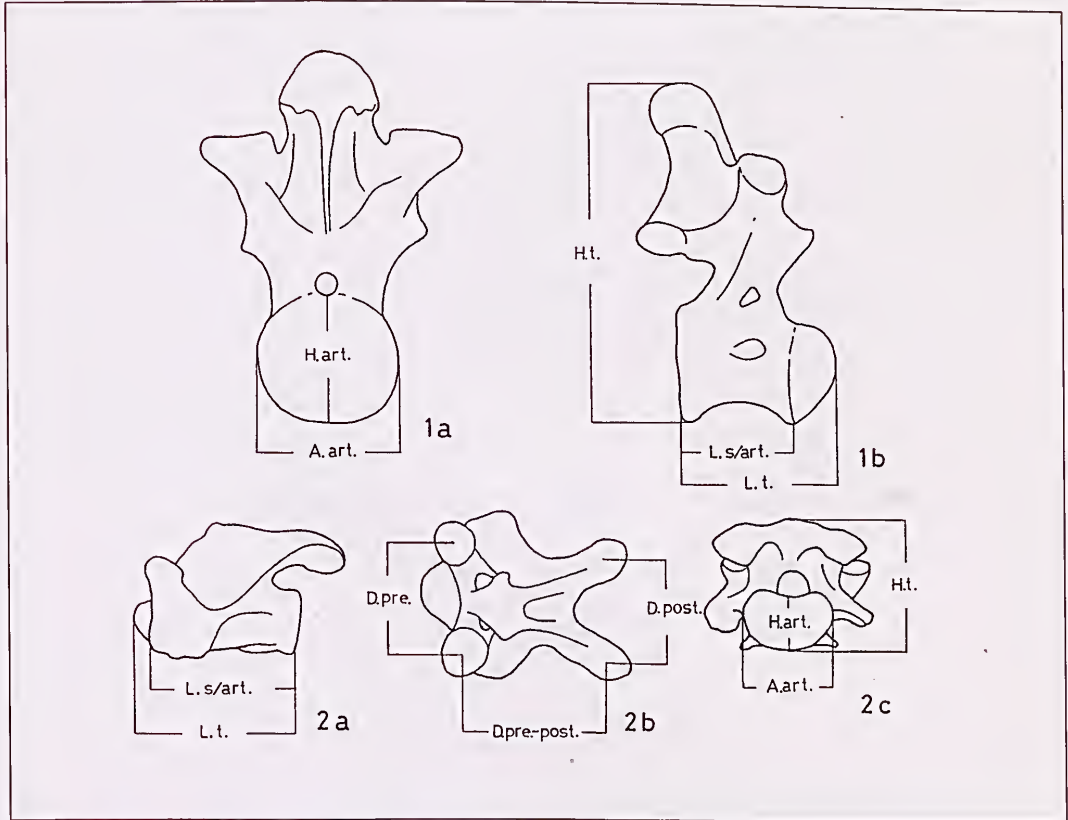


Plate 2. Principal measurements of the vertebrae

1. Dorsal vertebra in (a) posterior and (b) lateral views.

2. Cervical vertebra in (a) lateral, (b) dorsal, and (c) posterior views.

Abbreviations. A. art.: width of the articular surface; D. post.: distance between the centre of the articular facets of the postzygapophyses; D. pre.: distance between the centre of the articular facets of the prezygapophyses; D. pre. post.: distance between the articular facets of the prezygapophyses and postzygapophyses;

H. art.: height of the articular surface; H. t.: total height. L. s/art.: length of centrum between the anterior and posterior articular surfaces; L. t.: maximum length of centrum.

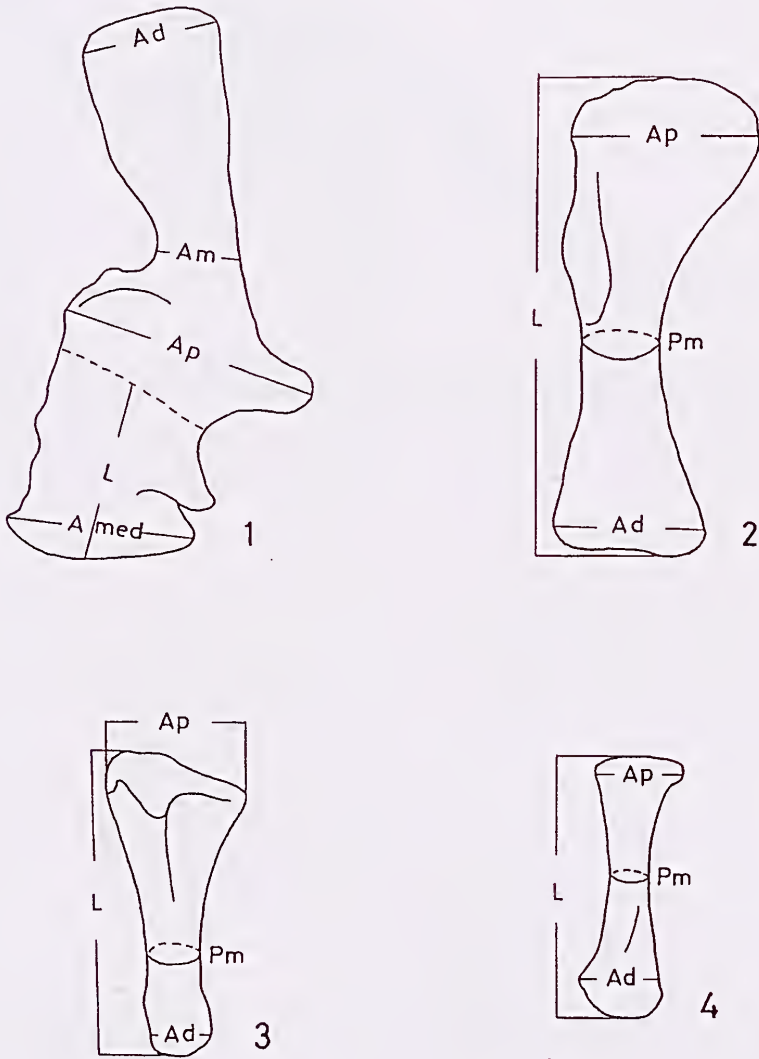


Plate 3. Principal measurements of the forelimb elements

1. Scapulo-coracoid

2. Humerus

3. Ulna

4. Radius

Abbreviations. Ad.: maximum distal width; Am.: minimum width; Amed.: width between the medial borders; Ap.: maximum proximal width; L: total length; Pm.: minimum perimeter of the cross-section of the shaft.

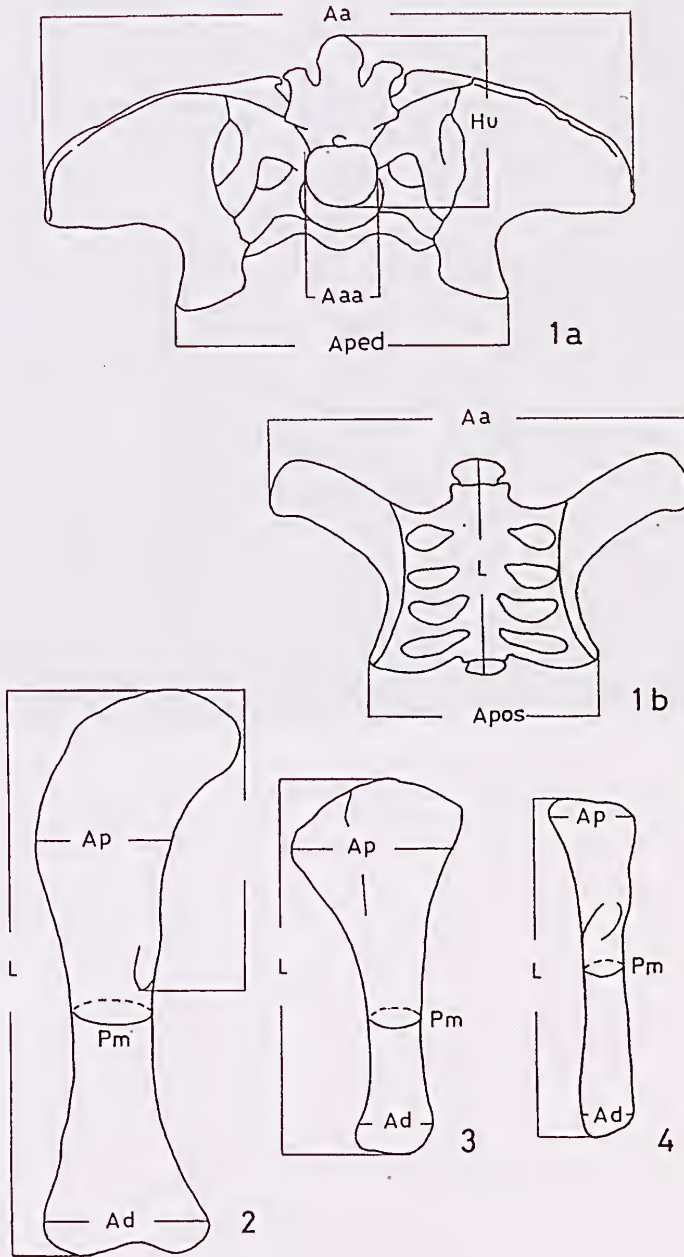


Plate 4. Principal measurements of the pelvic girdle and rear limb elements.

1. Sacrum articular with the ilium in (a) anterior and (b) dorsal views.

2. Femur

3. Tibia

4. Fibula

Abbreviations. Aa.: distance between the lateral extremities of the left and right ilia; Aaa.: width of the anterior articulation of the sacrum; Ad.: maximum distal width; Ap.: maximum proximal width; A. ped.: width between the pubic peduncles; A. pos.: width of the posterior articulation of the sacrum; Hu.: total height of the first sacral vertebra; Pm.: perimeter of the minimum cross section.



Plate 5. *Titanosaurus araukanicus* (Huene 1929a) n. comb.
1. Right tibia, MLP CS 1128, in (a) medial and (b) lateral stereoscopic views.
2. Right fibula, MLP CS 1127, in (a) lateral and (c) medial stereoscopic view and (b) posterior in monoscopic view.
3. Right scapula, MLP CS 1031, in (a) lateral and (b) dorsal stereoscopic views.
4. Cast of left fibula, BMNH R5935, in lateral stereoscopic view.

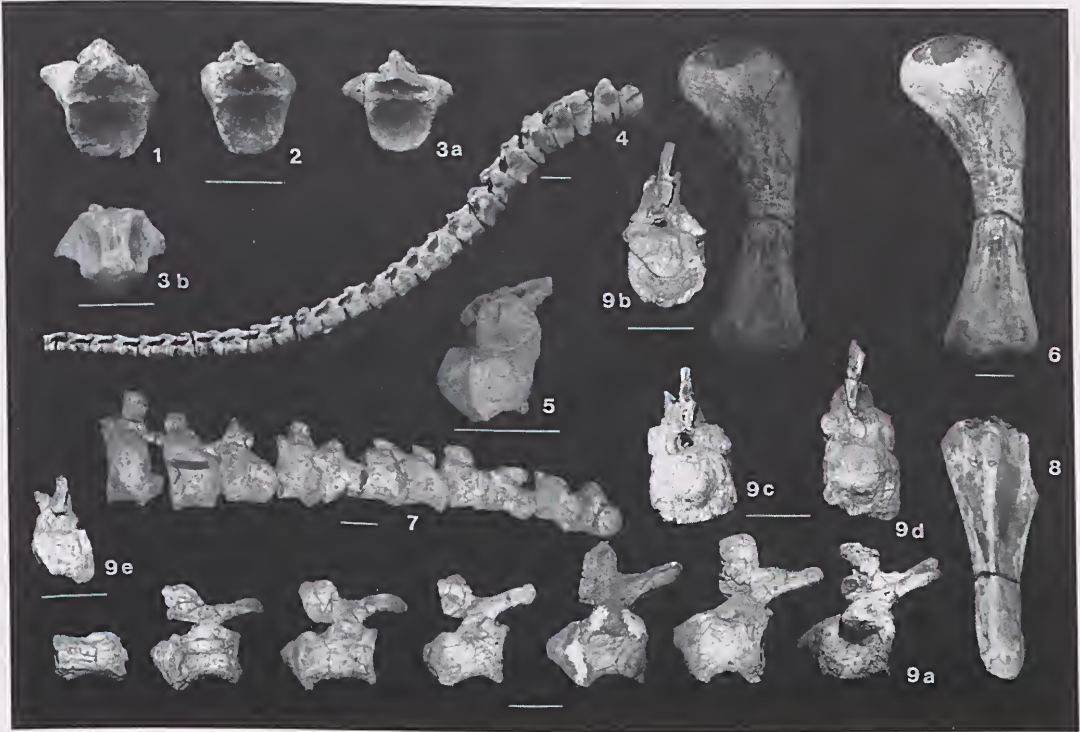


Plate 6. *Titanosaurus* sp.

1–2. Anterior caudal vertebrae, MPCA 1501, in anterior view

3. Caudal vertebrae, MPCA 1501, in (a) anterior and (b) ventral views.

4. Caudal vertebrae, MPCA 1501, in lateral view.

5. Anterior caudal vertebra, MPCA 1501, in lateral view

6. Right humerus, MLP Ly 15, in posterior view.

7. Articulated caudal vertebrae, MLP 26–28.

8. Right ulna of a juvenile individual, MLP CS 1058, in radial view.

Aeolosaurus rionegrinus?

9. Articulated series of extremely biconcave caudal vertebrae in (a) lateral view; anterior caudal vertebrae in (b–d) posterior view; and medial caudal vertebra in (e) posterior view.

Scale: 10 cm.

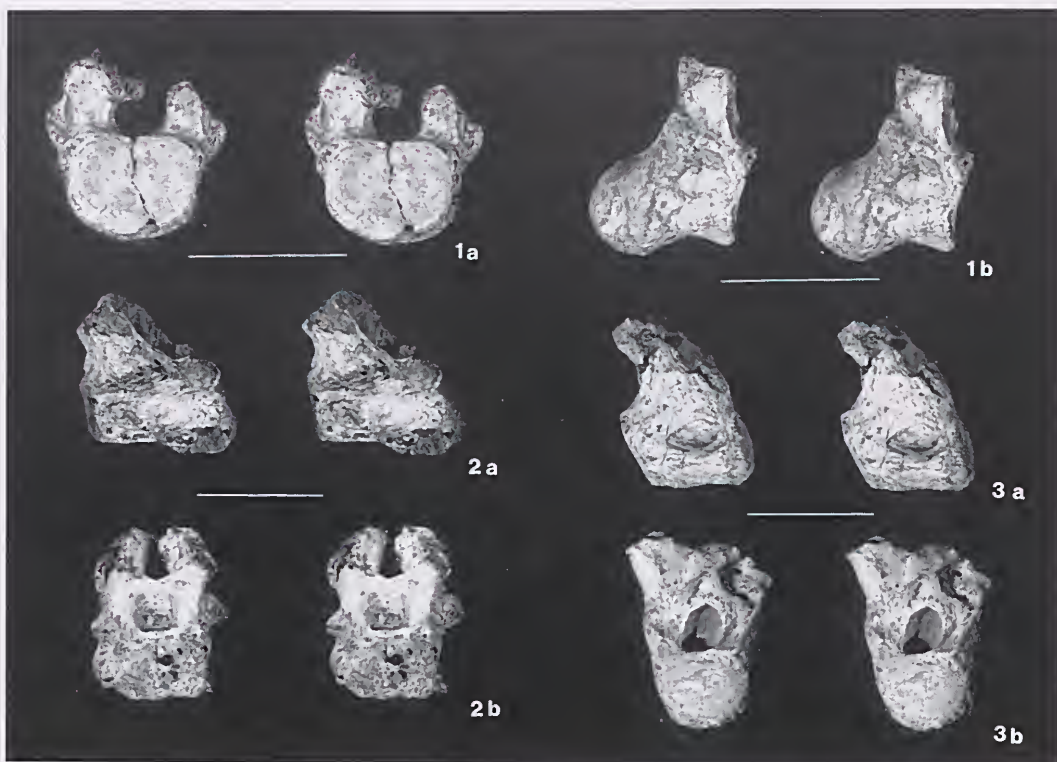


Plate 7. *Microcoelus patagonicus* Lydekker 1893 *n. dubium*

1. Anterior dorsal vertebra, MLP Ly 23 in stereoscopic (a) posterior and (b) lateral views.

Titanosaurus ? nanus Lydekker 1893 *n. dubium*

2. Posterior cervical vertebra, MLP Ly 18 in stereoscopic (a) lateral and (b) posterior views.

3. Dorsal vertebra, MLP Ly 19 in stereoscopic (a) lateral and (b) posterior view.

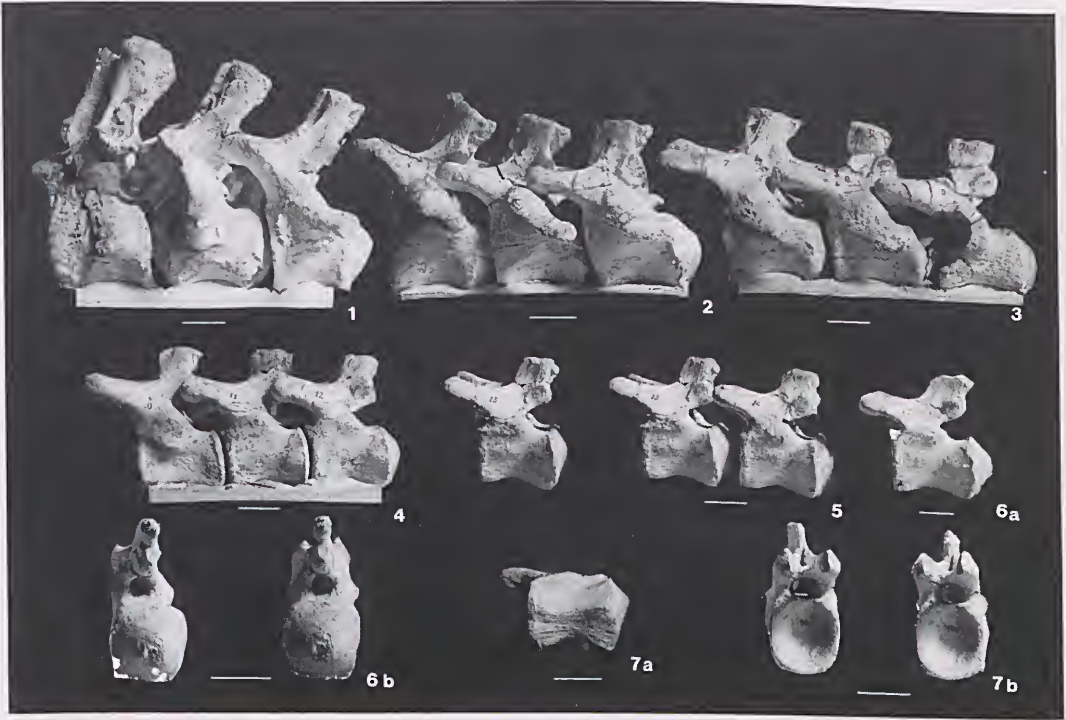


Plate 8. *cf. Titanosaurus* sp.

(Series C, from Peirópolis, Minas Geras State, Brazil)

1. Most posterior sacral vertebra plus first and second caudal vertebrae in lateral view.
2. Third, fourth, and fifth caudal vertebrae in lateral view. [Editor's note: The first vertebra of the series in Fig. 8.2 is designated in Spanish as 'Tercera' (third) despite the fact that the numeral four can clearly be seen on the illustration of this specimen. The discrepancy between the caption and the numbers written on the caudal vertebrae continues through and includes the caption for Fig. 8.7. This discrepancy in enumeration is due to the vertebrae having been numbered from the anteriormost found, which was the last sacral, not the first caudal.]
3. Sixth, seventh, and eighth caudal vertebrae in lateral view.
4. Ninth, tenth, and eleventh caudal vertebrae in lateral view.
5. Twelfth and thirteenth caudal vertebrae in lateral view. Twelfth vertebra in stereoscopic view.
6. Fourteenth caudal vertebra in (a) lateral view and in stereoscopic (b) posterior view.
7. Twelfth caudal vertebra in (a) ventral view and in stereoscopic (b) anterior view.

Scale: 5 cm.

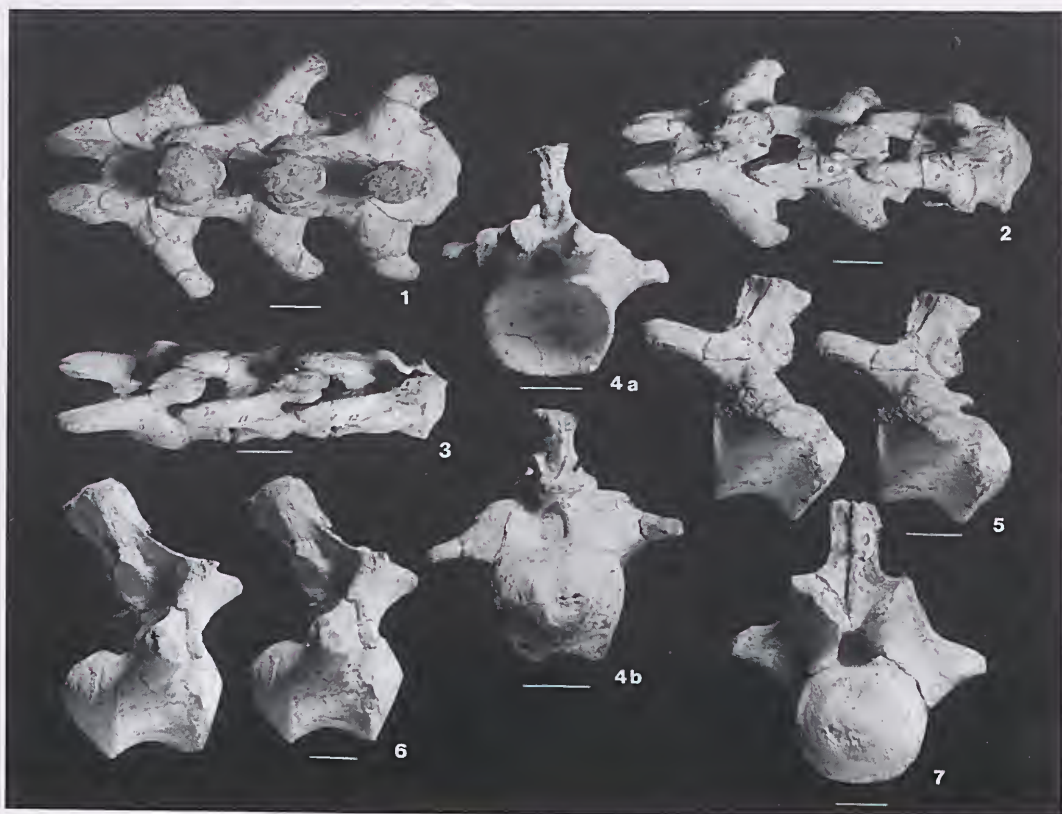


Plate 9. *Cf. Titanosaurus* sp.

(Series C, from Peirópolis, Minas Gerais State, Brazil)

1. Third, fourth, and fifth caudal vertebrae in dorsal view. [Editor's note: The first vertebra of the series in fig. 9.1 is designated in Spanish as 'Tercera' (third) despite the fact that the numeral four can clearly be seen on the illustration of this specimen. The discrepancy between the caption and the numbers written on the caudal vertebrae continues through and includes the caption for fig. 9.3. This discrepancy in enumeration is due to the vertebrae having been numbered from the anteriormost found, which was the last sacral, not the first caudal.]

2. Sixth, seventh, and eighth caudal vertebrae in dorsal view.

3. Ninth, tenth, and eleventh caudal vertebrae in dorsal view.

4. Second caudal vertebra in (a) anterior and (b) posterior view.

5. Second caudal vertebra in left lateral stereoscopic view.

6. First caudal vertebra in right lateral stereoscopic view.

7. First caudal vertebra in anterior view.

Scale: 5 cm.

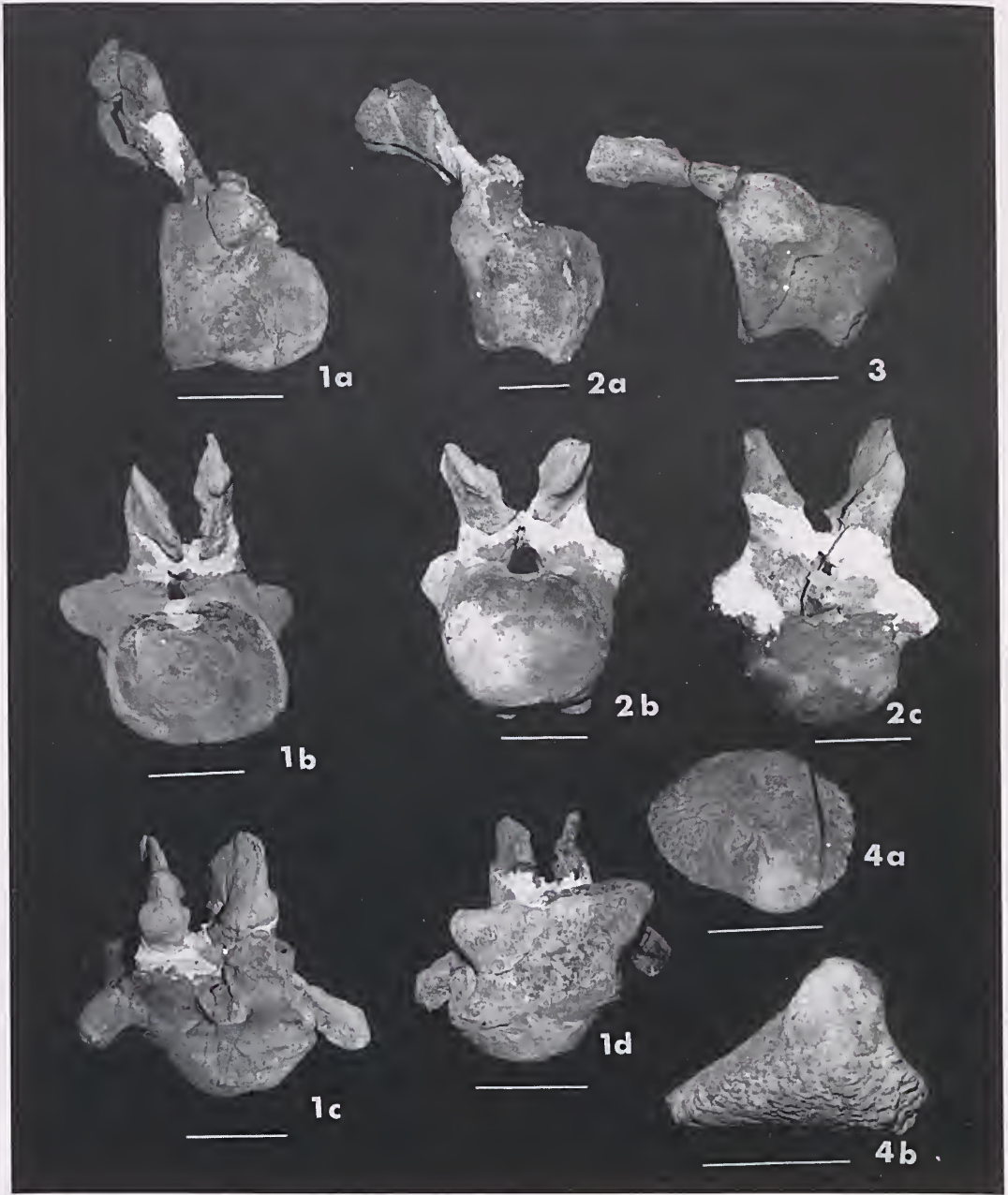


Plate 10. *Aeolosaurus rionegrinus* n. gen. et n. sp.
(MJG – R 1. Holotype)

1. Third? caudal vertebra in (a) lateral, (b) anterior, (c) dorsal, and (d) ventral views.

2. Fourth? caudal vertebra in (a) lateral, (b) anterior, and (c) dorsal views.

3. Sixth caudal vertebra in lateral view.

4. Right astragalus in (a) dorsal and (b) posterior views.

Scale 10 cm.

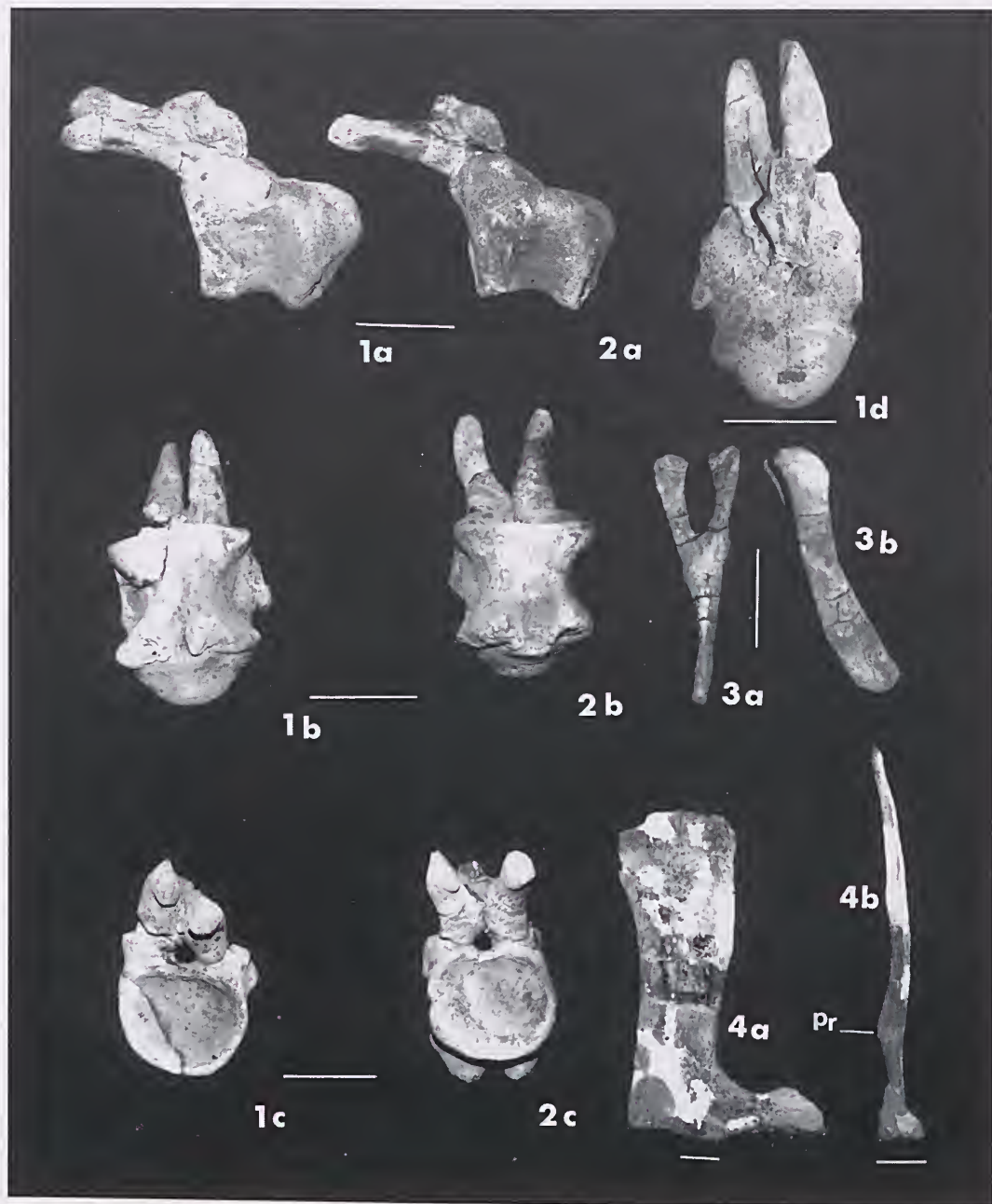


Plate 11. *Aeolosaurus rionegrinus* n. gen. et n. sp.
(MJG - R 1. Holotype)

1. Seventh? caudal vertebra in (a) lateral, (b) ventral, (c) anterior, and (d) dorsal views.

2. Eighth? caudal vertebra in (a) lateral, (b) ventral, and (c) anterior views.

3. Hemapophysis in (a) posterior and (b) lateral views.

4. Right scapula in (a) lateral and (b) dorsal views.

Abbreviation. Pr.: process for muscular attachment.

Scale: 10 cm.



Plate 12. *Aeolosaurus rionegrinus* n. gen. et n. sp.
(MJG – R 1. Holotype)

1. Right humerus in anterior view.
 2. Left humerus in (a) anterior and (b) lateral views.
 3. Right ulna in radial view.
 4. Right radius in (a) dorso-medial, and (b) ventro-lateral view.
 5. Right ischium in (a) dorsomedial and (b) ventrolateral views.
 6. Left ischium in (a) dorsomedial and (b) ventrolateral views.
 7. Left tibia in lateral view.
 8. Right fibula in (a) lateral and (b) tibial views.
- Scale: 10 cm.

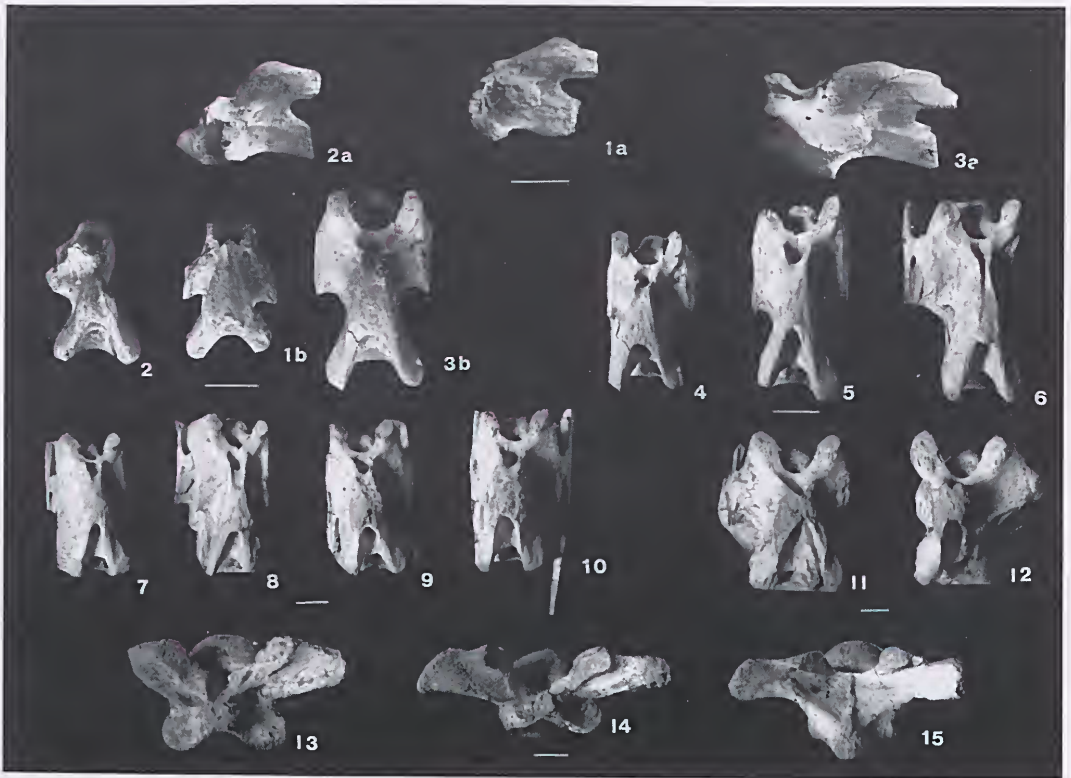


Plate 13. Titanosaurinae indet.

(Series A from Peirópolis, Minas Gerais State, Brazil)

1. Axis in (a) lateral and (b) dorsal views.
2. Third cervical vertebra in (a) lateral and (b) dorsal views.
3. Fourth cervical vertebra in (a) lateral and (b) dorsal views.
4. Fourth cervical vertebra in dorsal view.
5. Fifth cervical vertebra in dorsal view.
6. Sixth cervical vertebra in dorsal view.
7. Seventh cervical vertebra in dorsal view.
8. Eighth cervical vertebra in dorsal view.
9. Ninth cervical vertebra in dorsal view.
10. Tenth cervical vertebra in dorsal view.
11. Eleventh cervical vertebra in dorsal view.
12. Twelfth cervical vertebra in dorsal view.
13. First dorsal vertebra in dorsal view
14. Second dorsal vertebra in dorsal view.
15. Third dorsal vertebra in dorsal view.

Scale: 5 cm.



Plate 14. Titanosaurinae indet.

(Peirópolis, Minas Gerais State, Brasil)

Series A

1. Seventh cervical vertebra and fragment of the articulating rib in lateral view.
2. Tenth cervical vertebra with complete articulating rib in lateral view.
3. Eighth cervical vertebra in lateral view.
4. Ninth cervical vertebra in lateral view.

Series B

5. Twelfth cervical vertebra in right lateral view.

Series A

6. Twelfth cervical vertebra in left lateral view.
7. Thirteenth cervical vertebra in anterior view.
8. First dorsal vertebra in anterior view.
9. Second dorsal vertebra in anterior view.

Scale: 5 cm.

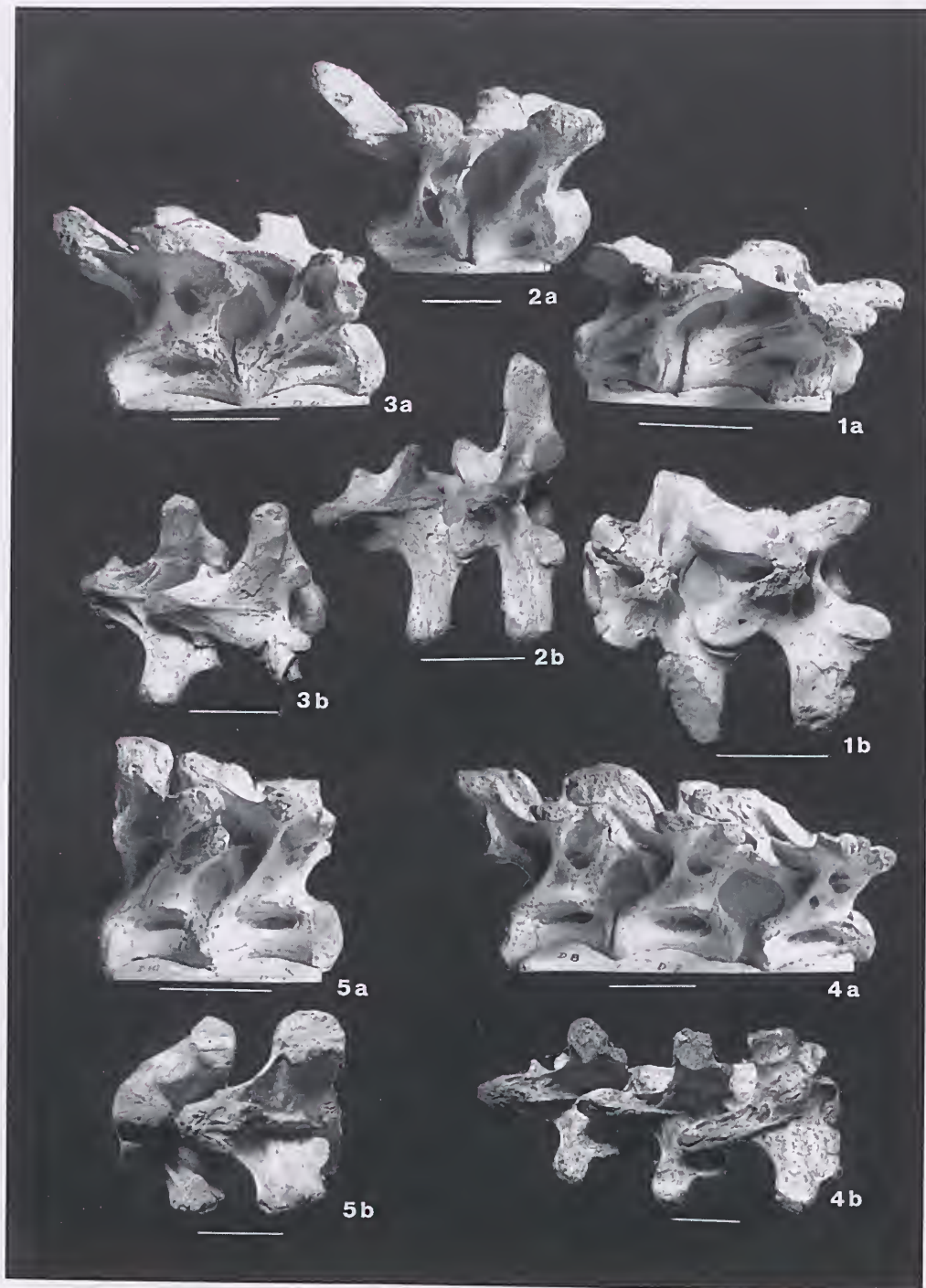


Plate 15. Titanosaurinae indet.

(DGM Series B from Peirópolis, Minas Gerais State, Brazil)

1. Most posterior cervical vertebra and first dorsal vertebra in (a) lateral and (b) dorsal views.

2. Second dorsal vertebra in (a) lateral and (b) dorsal views.

3. Fourth and fifth dorsal vertebrae in (a) lateral and (b) dorsal views.

4. Sixth, seventh and eighth dorsal vertebrae in (a) lateral and (b) dorsal views.

5. Ninth and tenth dorsal vertebrae in (a) lateral and (b) dorsal views.

Scale: 10 cm.

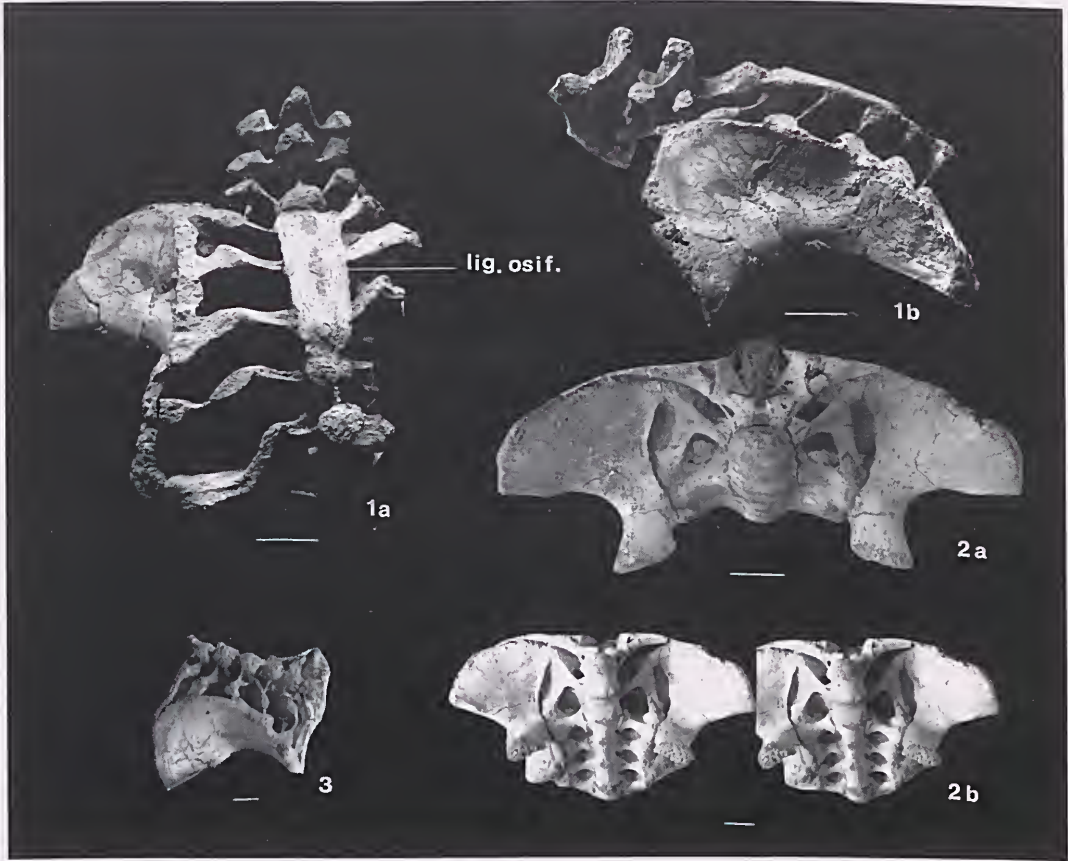


Plate 16. Titanosaurinae indet.

(Peirópolis, Minas Gerais State, Brazil)

1. Sacrum in articulation with the left ilium in (a) posterior and (b) lateral views. Note the ossified ligaments. MCT 1489-R.

2. Sacrum with both ilia articulated in (a) anterior and (b) stereoscopic anteroventral views. MCT 1536-R.

3. Sacrum with left ilium articulated in laterodorsal view. MCT 1488-R.

[*Editor's note:* these three pelvises are described and illustrated in Campos and Kellner (1999).]

Abbreviation. Lig. osif.: Ossified tendons.

Scale: 10 cm.

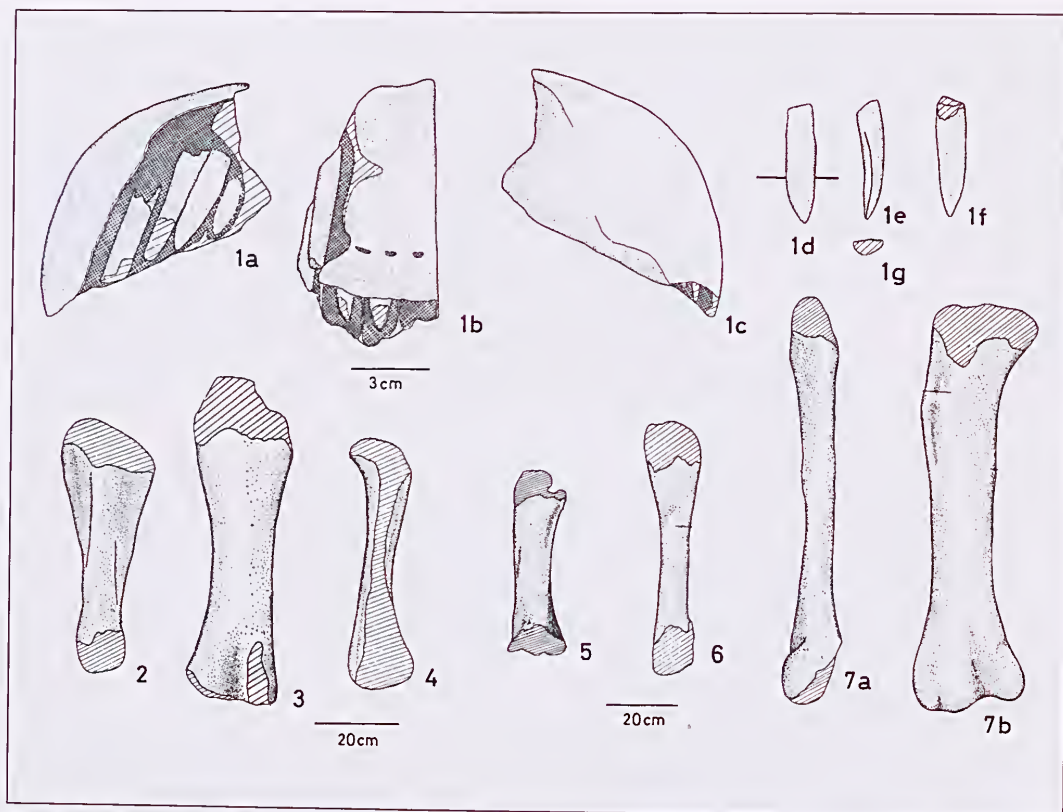


Plate 17. Titanosauridae indet.

(Arroyo Morterito, Province of Salta, Argentina)

1. Left premaxilla, PVL 3670-12, in (a) lateral, (b) medial, and (c) lingual views. Teeth from that same premaxilla in (d) labial, (e) medial, (f) and lingual views and in (g) transverse section.
2. Right ulna, PVL 3670-2, in anterolateral view.
3. Right humerus, PVL 3670-1, in posterior view.
4. Right radius, PVL 3670-3, in ulnar view.
5. Fragment of right tibia, PVL 3670-5, in fibular view.
6. Right fibula, PVL 3670-6, in lateral view.
7. Left femur, PVL 3670-4, in (a) medial and (b) posterior views.



Plate 18. Reconstruction of *Saltasaurus loricatus* Bonaparte and Powell 1980, an armoured titanosaur from the Late Cretaceous El Brete locality, Salta Province, Argentina.

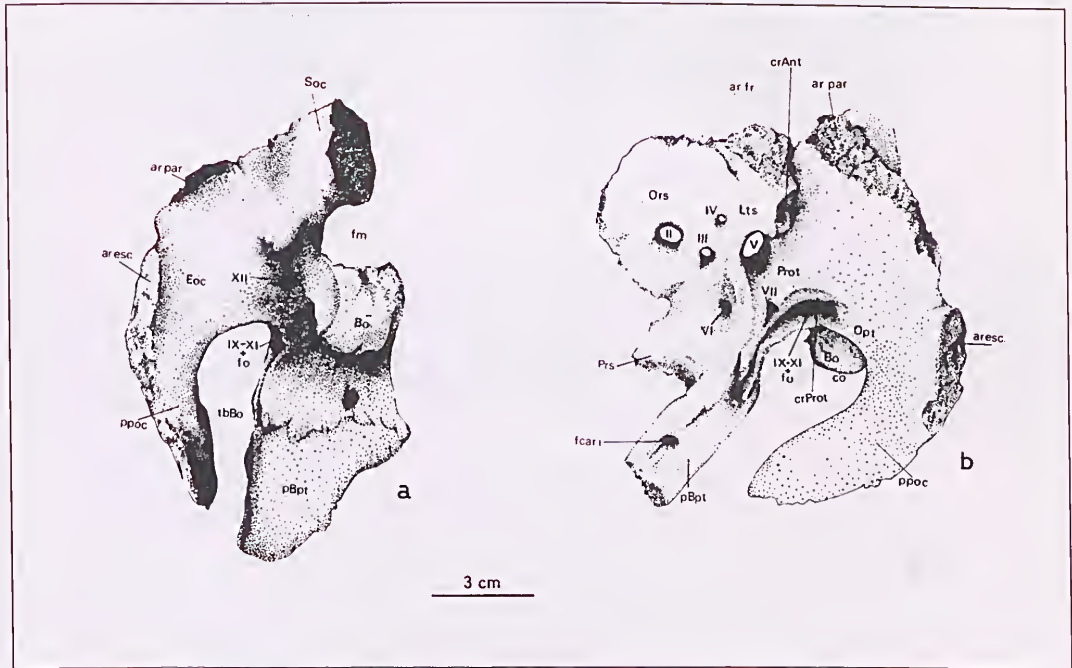


Plate 19. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Fragment of the skull, PVL 4017-161, in (a) posterior and (b) lateral views.

Abbreviations. aresc.: superficial articulation with the squamosal; ar fr.: superficial articulation with the frontal; ar par.: superficial articulation with the parietal; Bo.: basioccipital; co: occipital condyle; crAnt.: crista antotica; crProt.: crista prootica; Eoc.: exoccipital; fcarl.: internal carotid foramen; fm.: foramen magnum; fo.: fenestra ovalis; Lts.: laterosphenoid; Opt.: opisthotic; Ors.: orbitosphenoid; pBpt.: basiptyergoid process; ppoc.: paraoccipital process; Prot.: prootic; Prs.: presphenoid; Soc.: supraoccipital; tbBo.: basal tuberosity of the basioccipital.

Drawn by A Castillo.

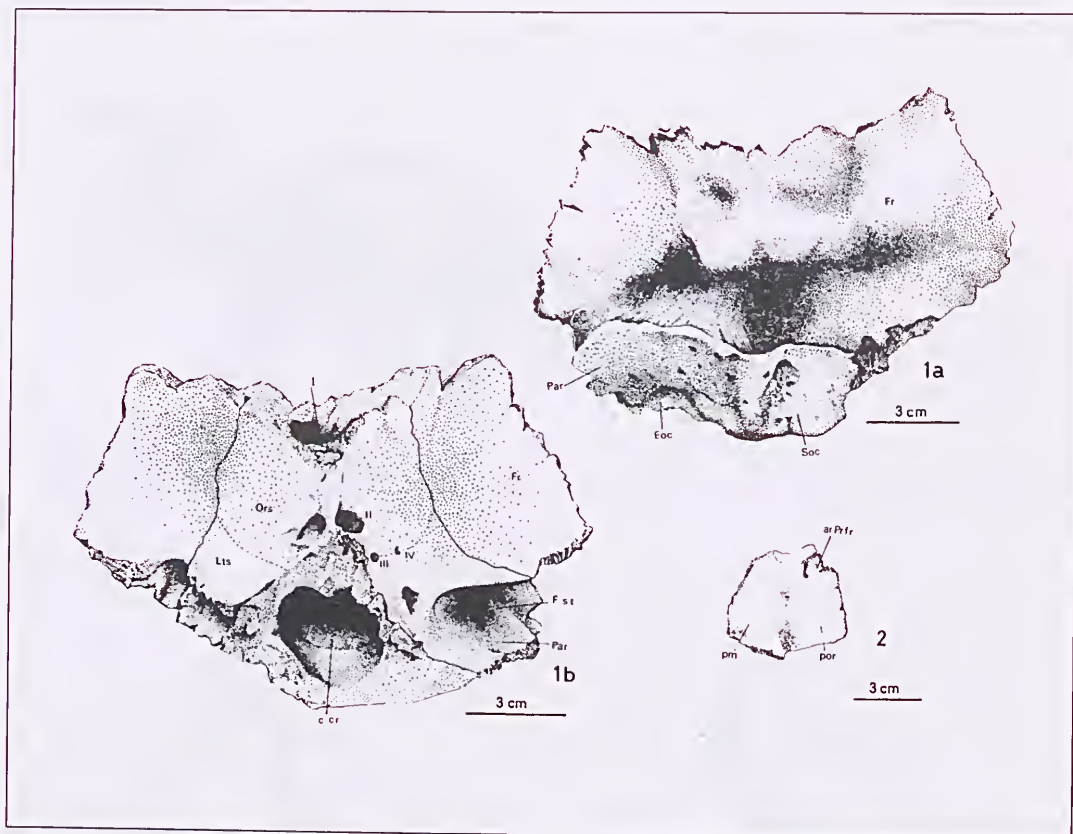


Plate 20. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Fragment of the skull, PVL 4017-162, in (a) ventral and (b) dorsal views.

2. Juvenile? right frontal, PVL 4017-211.

Abbreviations. ar. Prfr.: area of articulation with the prefrontal; c. cr.: cranial cavity; Eoc.: exoccipital; Fr.: frontal; F. s. t.: supratemporal aperture; Lts.: laterosphenoid; Ors.: orbitosphenoid; Par.: parietal; pm.: medial moiety; por.: orbital moiety; Soc.: supraoccipital.

Drawn by A Castillo.

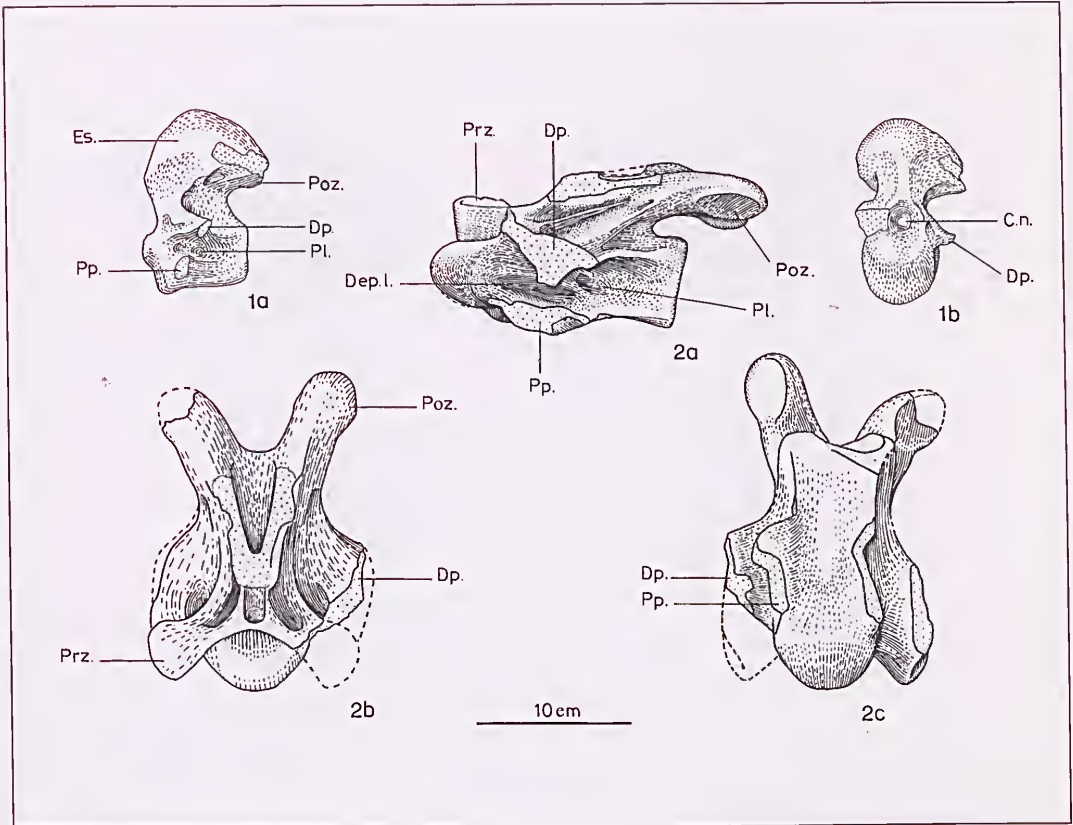


Plate 21. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Axis, PVL 4017-1, in (a) ventral and (b) anterior views.

2. Anterior cervical vertebra, PVL 4017-3, in (a) lateral, (b) dorsal, and (c) ventral views.

Abbreviations. C. n.: neural canal; Dep. l.: lateral depression; Dp.: diapophysis; Es.: neural spine; Pl.: pleurocoel; Poz.: postzygapophysis; Pp.: parapophysis; Prz.: prezygapophysis.

Drawn by E. Guanuco.

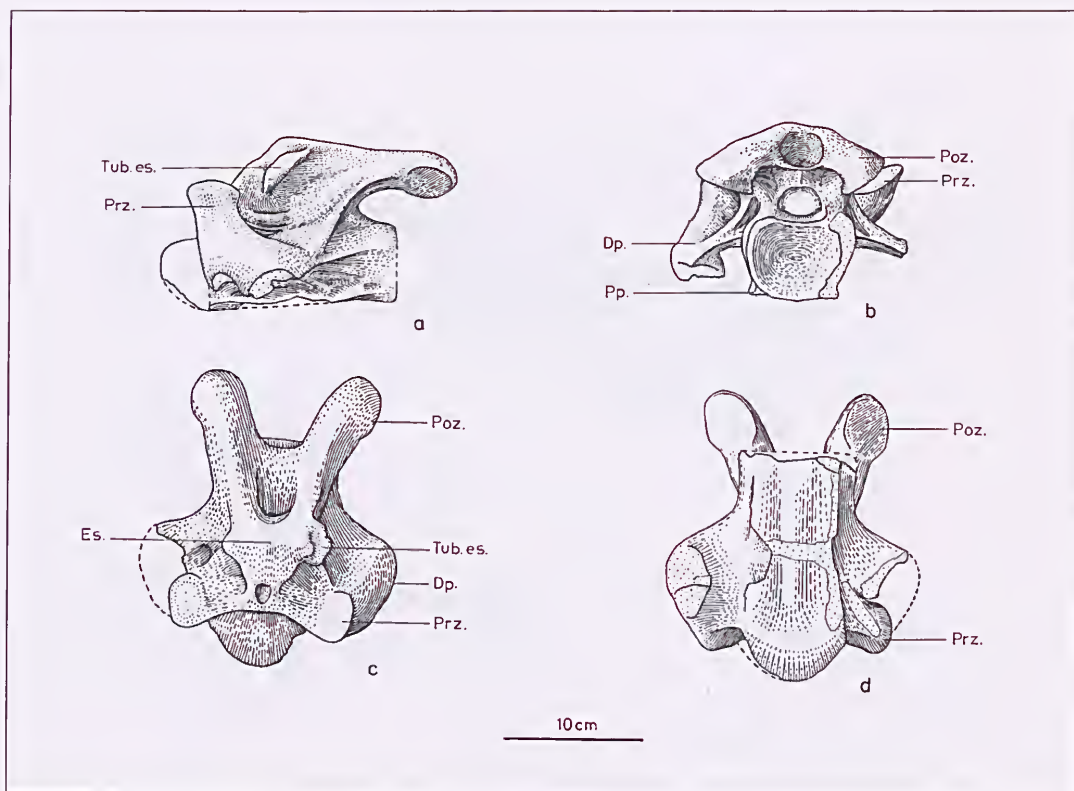


Plate 22. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Anterior cervical vertebra, PVL 4017-139, in (a) lateral, (b) posterior, (c) dorsal, and (d) ventral views.

Abbreviations. Dp.: diapophysis; Es.: neural spine; Poz.: postzygapophysis; Pp.: parapophysis; Prz.: prezygapophysis; Tub. es.: tuberosity of the neural spine.

Drawn by E Guanuco.

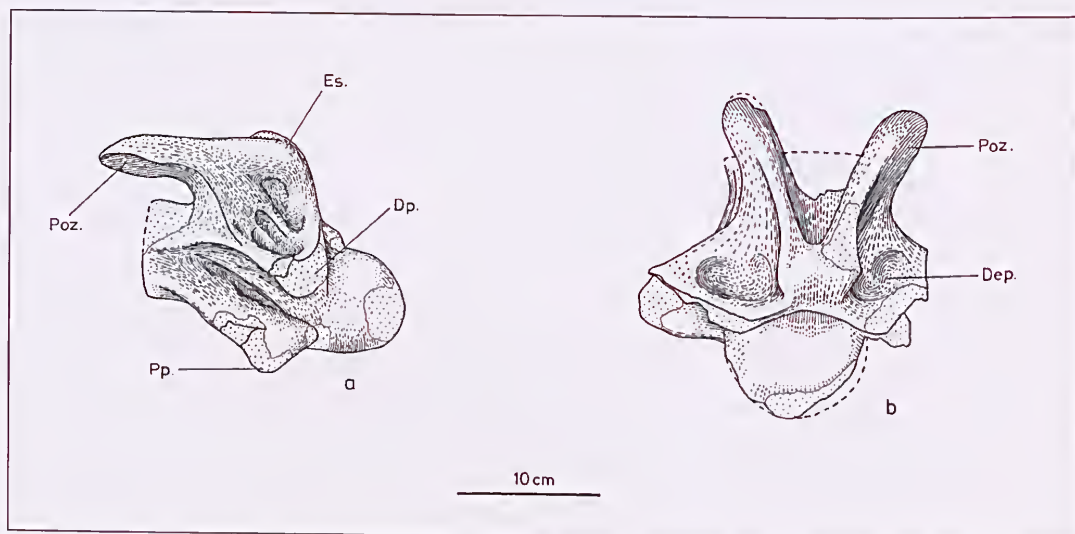


Plate 23. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Posterior cervical vertebra, PVL 4017-6, in (a) lateral, and (b) dorsal views.

Abbreviations. Dep.: depression; Dp.: diapophysis; Es.: neural spine; Poz.: postzygapophysis; Pp.: parapophysis.

Drawn by E Guanuco.

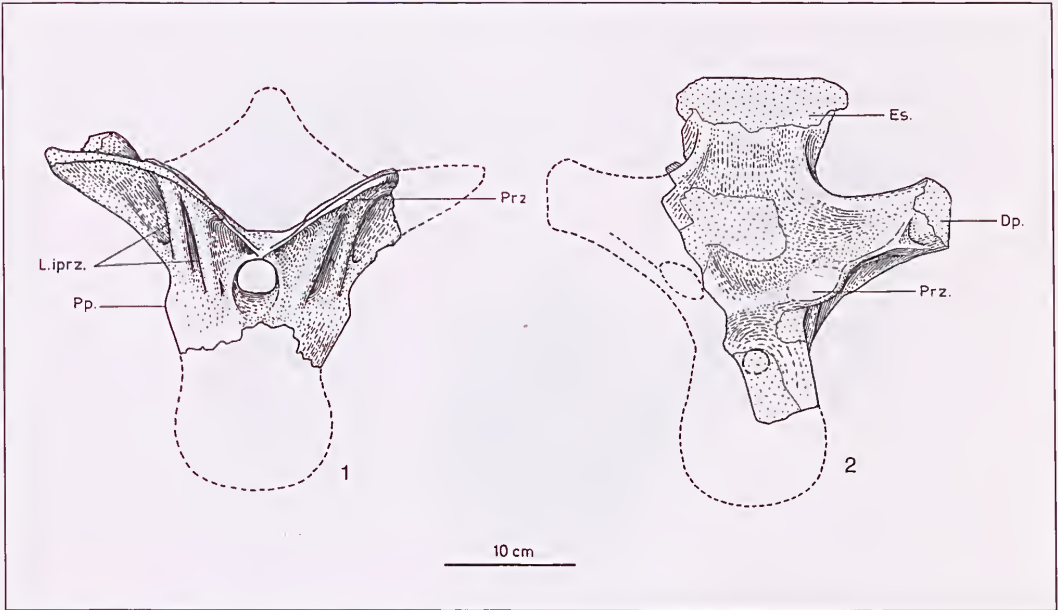


Plate 24. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. First? dorsal vertebra, PVL 4017-10, in anterior view.

2. Second or third dorsal vertebra, PVL 4017-12, in anterior view.

Abbreviations. Dp.: diapophysis; Es.: neural spine; L. iprz.: infraprezygapophyseal lamina; Pp.: parapophysis; Prz.: prezygapophysis.

Drawn by E Guanuco.

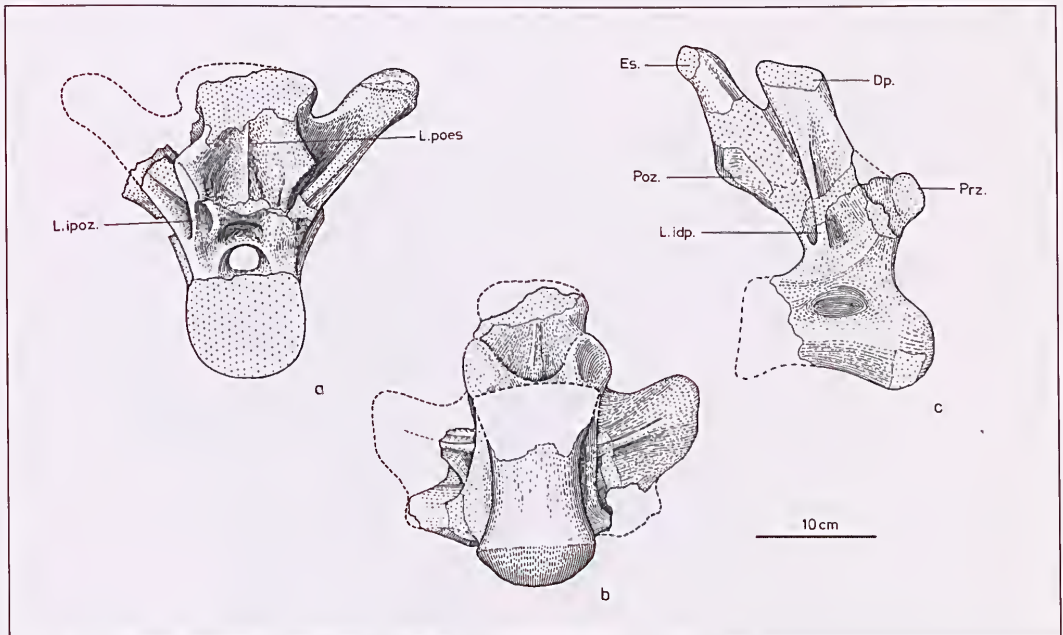


Plate 25. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Anterior dorsal vertebra, PVL 4017-11, in (a) posterior, (b) ventral, and (c) lateral views.

Abbreviations. Dp.: diapophysis; Es.: neural spine; L. idp.: infradiapophyseal lamina; L. ipoz.: infrapostzygapophyseal lamina; L. poes.: postspinal lamina; Poz.: postzygapophysis; Prz.: prezygapophysis.

Drawn by E Guanuco.

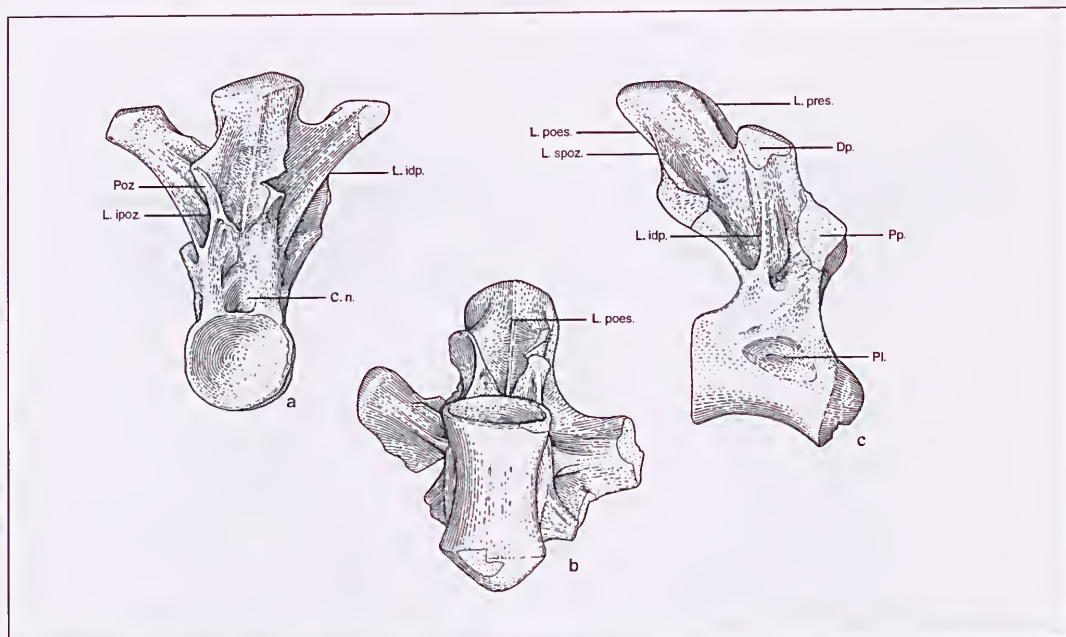


Plate 26. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Dorsal vertebra, PVL 4017-14, in (a) posterior, (b) ventral, and (c) lateral views.

Abbreviations. C. n. neural canal; Dp.: diapophysis; L. idp.: infradiapophyseal lamina;

L. ipoz.: infrapostzygapophyseal lamina; L. poes.: postspinal lamina; L. pres.: prespinal lamina;

L. spoz.: suprapostzygapophyseal lamina; Pl.: pleurocoel; Poz.: postzygapophysis; Pp.: parapophysis.

Drawn by E Guanuco.

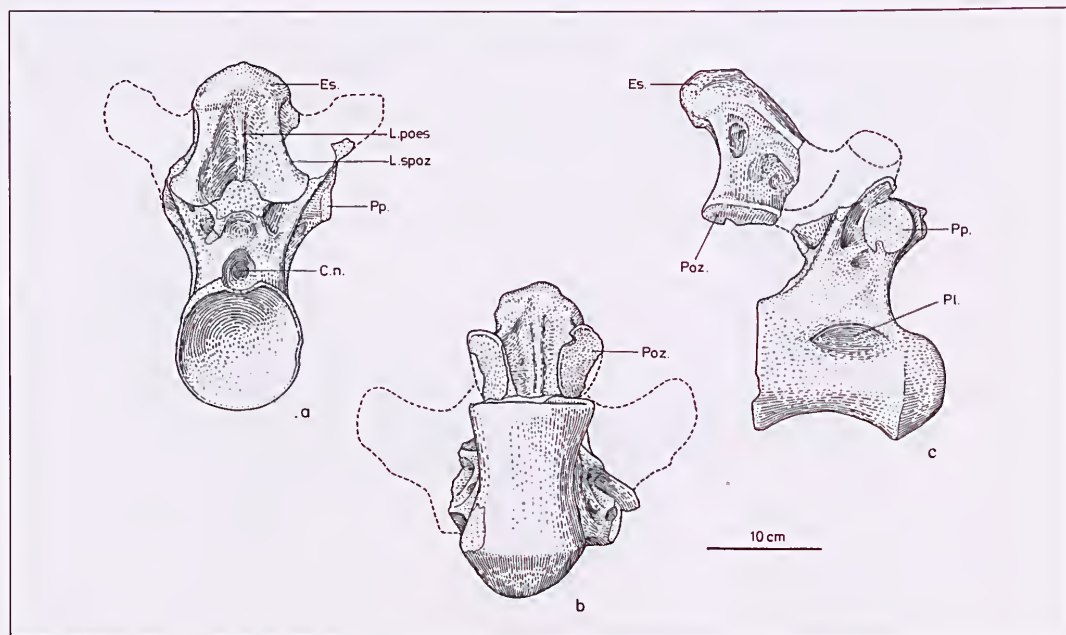


Plate 27. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Posterior dorsal vertebra, PVL. 4017-137, in (a) posterior, (b) lateral, and (c) ventral views.

Abbreviations. C. n. neural canal; Es.: neural spine; L. poes.: postspinal lamina; Pl.: pleurocoel; Poz.: postzygapophysis; Pp.: parapophysis.

Drawn by E Guanuco.

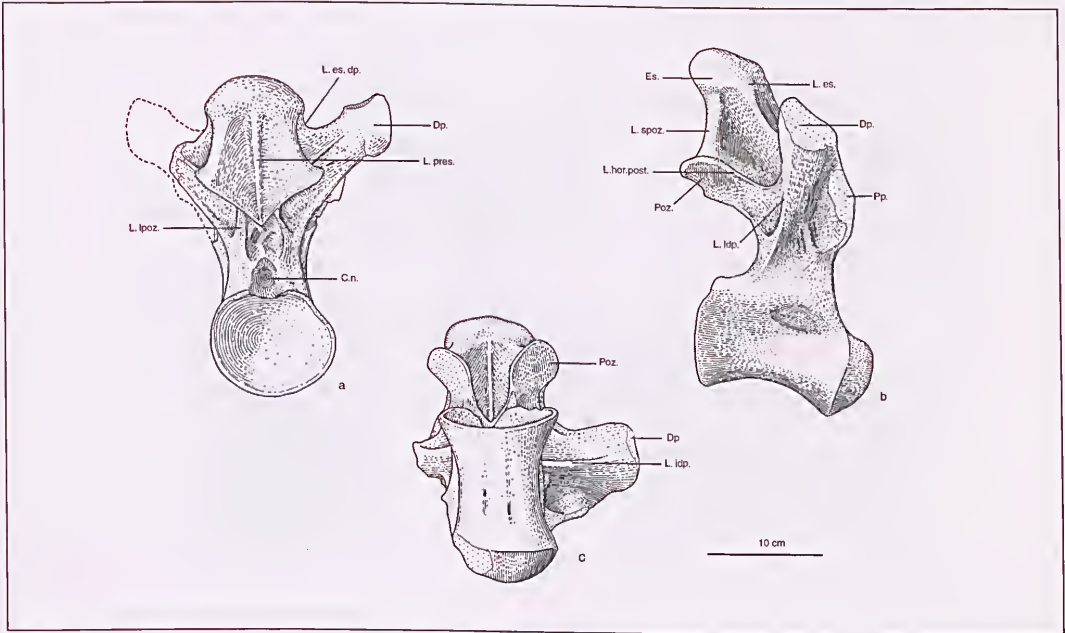


Plate 28. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Posterior dorsal vertebra, PVL 4017-136, in (a) posterior, (b) ventral, and (c) lateral views.

Abbreviations. C. n. neural canal; Dp.: diapophysis; Es.: neural spine; L. es. = L. es. dp.: lamina of the diapophyseal spine; L. hor. post.: posterior horizontal lamina; L. idp.: infradiapophyseal lamina; L. ipoz.: infrapostzygapophyseal lamina; L. pres.: prespinal lamina; L. spoz.: suprapostzygapophyseal lamina; Pl.: pleurocoel; Poz.: postzygapophysis; Pp.: parapophysis. Drawn by E Guanuco.

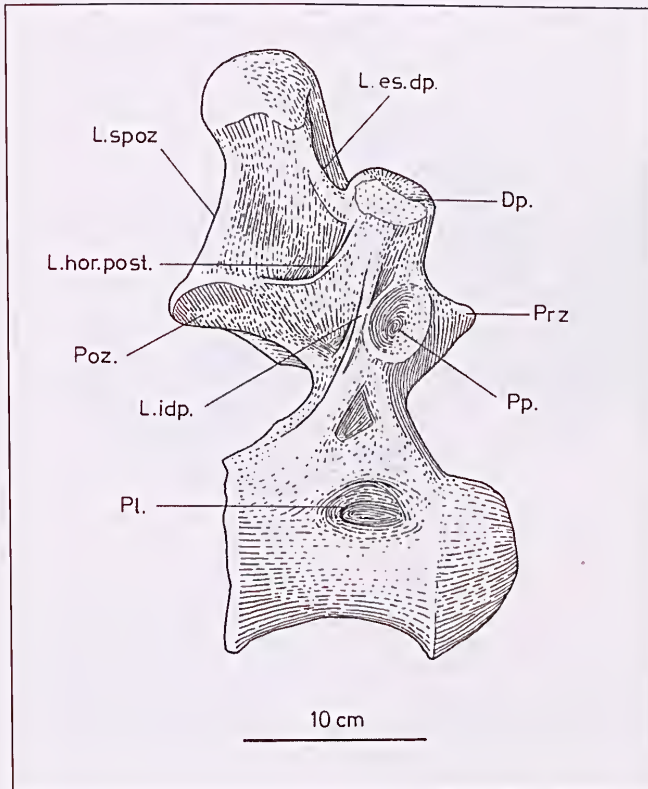


Plate 29. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Posterior dorsal vertebra, PVL 4017-135, in lateral view.

Abbreviations. Dp.: diapophysis; L. es. dp.: lamina of the diapophyseal spine; L. hor. post.: posterior horizontal lamina; L. idp.: infradiapophyseal lamina; L. spoz.: suprapostzygapophyseal lamina; Pl.: pleurocoel; Poz.: postzygapophysis; Pp.: parapophysis; Prz.: prezygapophysis. Drawn by E Guanuco.

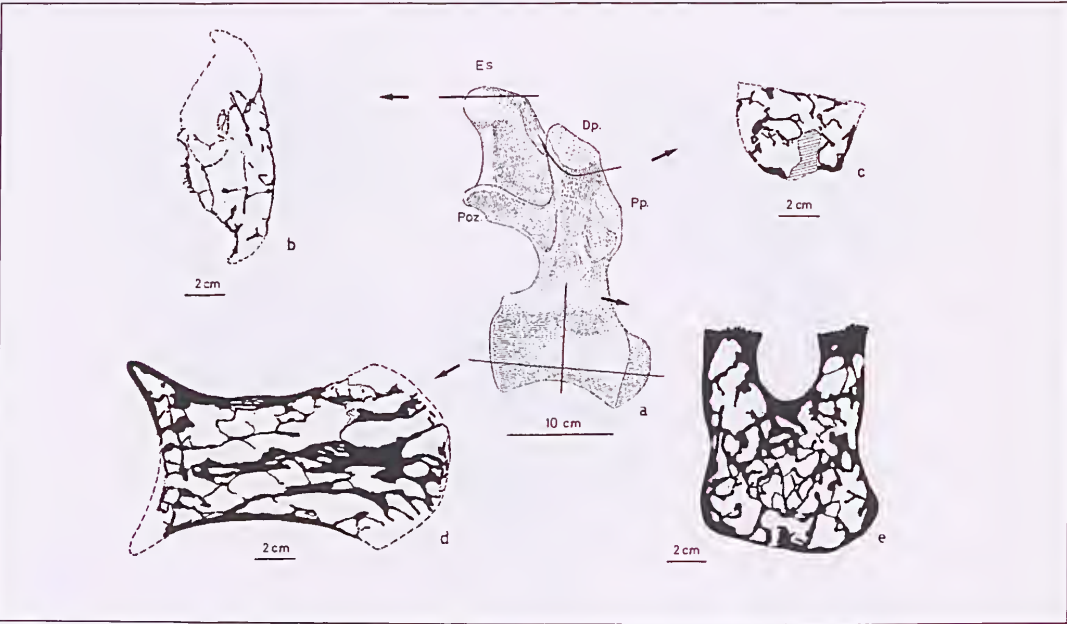


Plate 30. *Saltasaurus loricatus* Bonaparte and Powell 1980.
a. Posterior dorsal vertebra, PVL 4017-137, showing the location of the polished sections in the various dorsal vertebrae, in which can be seen the complicated development of the bony laminae.
b. Section of the neural spine of the dorsal vertebra PVL 4017-137.
c. Section of the tip of the diapophysis of the dorsal vertebra PVL 4017-137.
d. Frontal section of the centrum of the dorsal vertebra PVL 4017-43
e. Transverse section of the centrum of the dorsal vertebra PVL 4017-47.
Abbreviations. Dp.: diapophysis; Es.: neural spine; Pp.: pleurocoel.

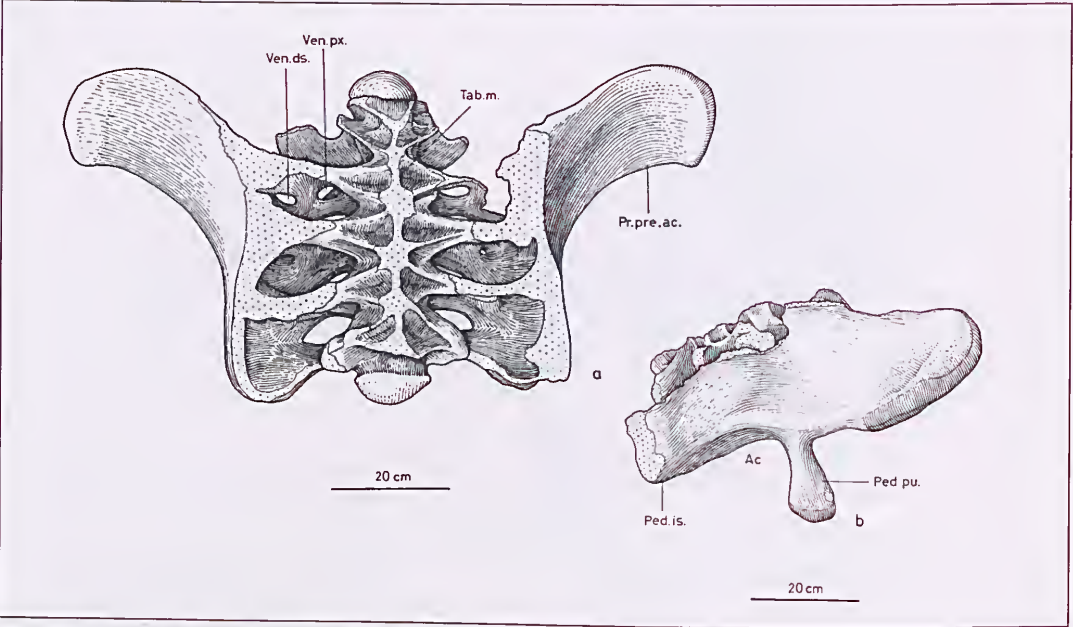


Plate 31. *Saltasaurus loricatus* Bonaparte and Powell 1980.
Sacrum articulated with both ilia, PVL 4017-92, in (a) dorsal and (b) lateral views.
Abbreviations. Ac.: acetabulum; Ped. Is.: ischia peduncle; Ped. Pu.: pubic peduncle; Pr. pre. ac.: preacetabular process of the iliac lamina; Tab. m.: medial wall; Ven. ds.: distal fenestra; Ven. px.: proximal fenestra.
Drawn by E Guanuco.

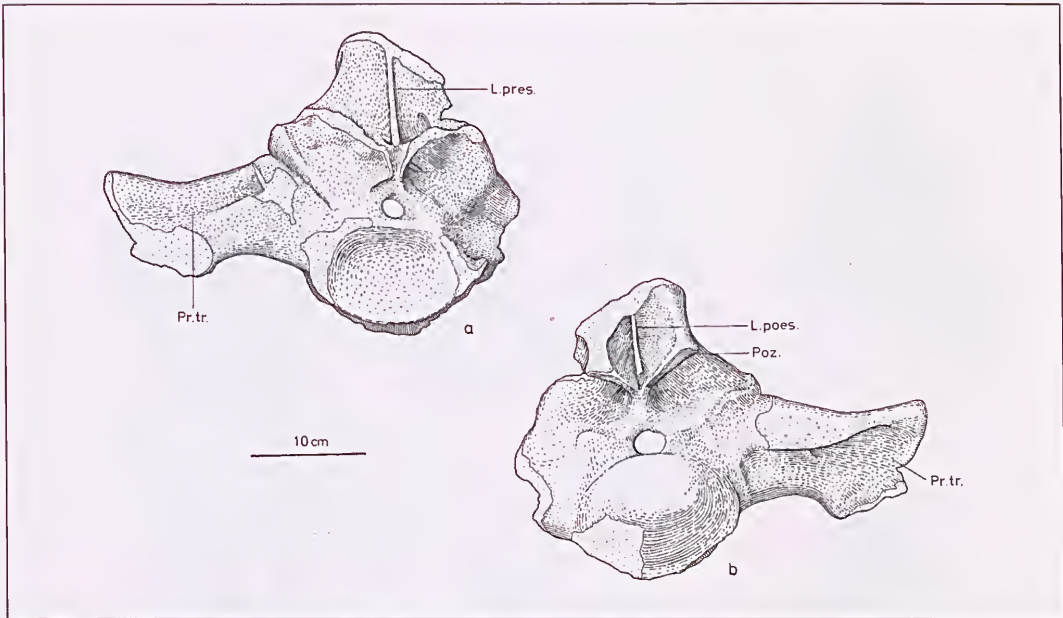


Plate 32. *Saltasaurus loricatus* Bonaparte and Powell 1980.

First caudal vertebra, PVL 4017-19, in (a) anterior and (b) posterior views.

Abbreviations. L. poes.: postspinal lamina; L. pres.: prespinal lamina; Poz.: postzygapophysis; Pr. tr.: transverse process.

Drawn by E Guanuco.

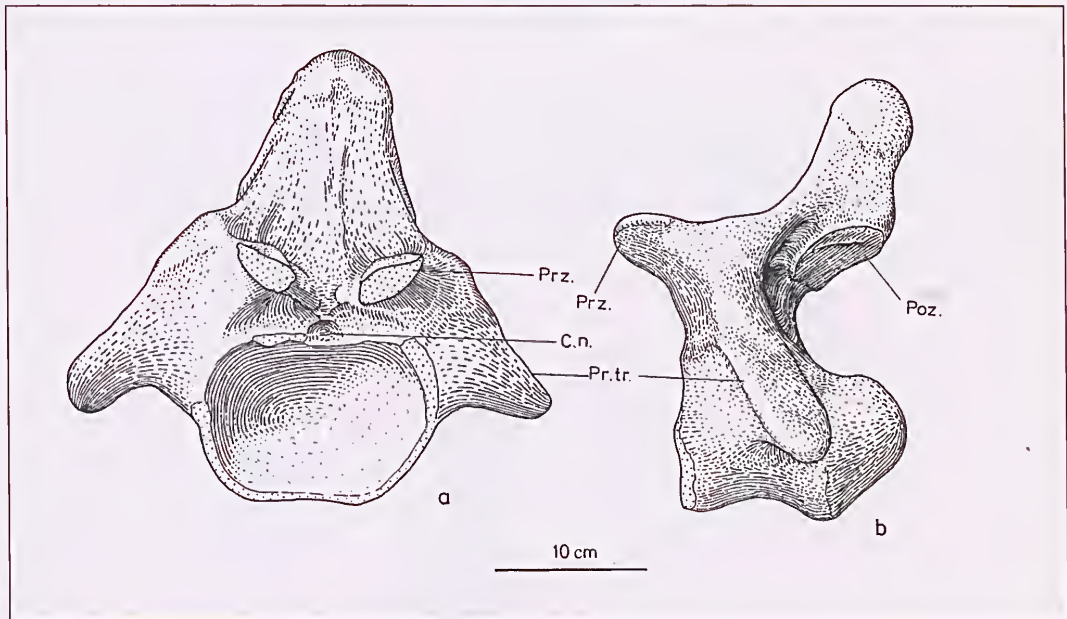


Plate 33. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Anterior caudal vertebra, PVL 4017-23, in (a) anterior and (b) lateral views.

Abbreviations. C. n.: neural canal; Poz.: postzygapophysis; Pr. tr.: transverse process; Prz.: prezygapophysis.

Drawn by E Guanuco.

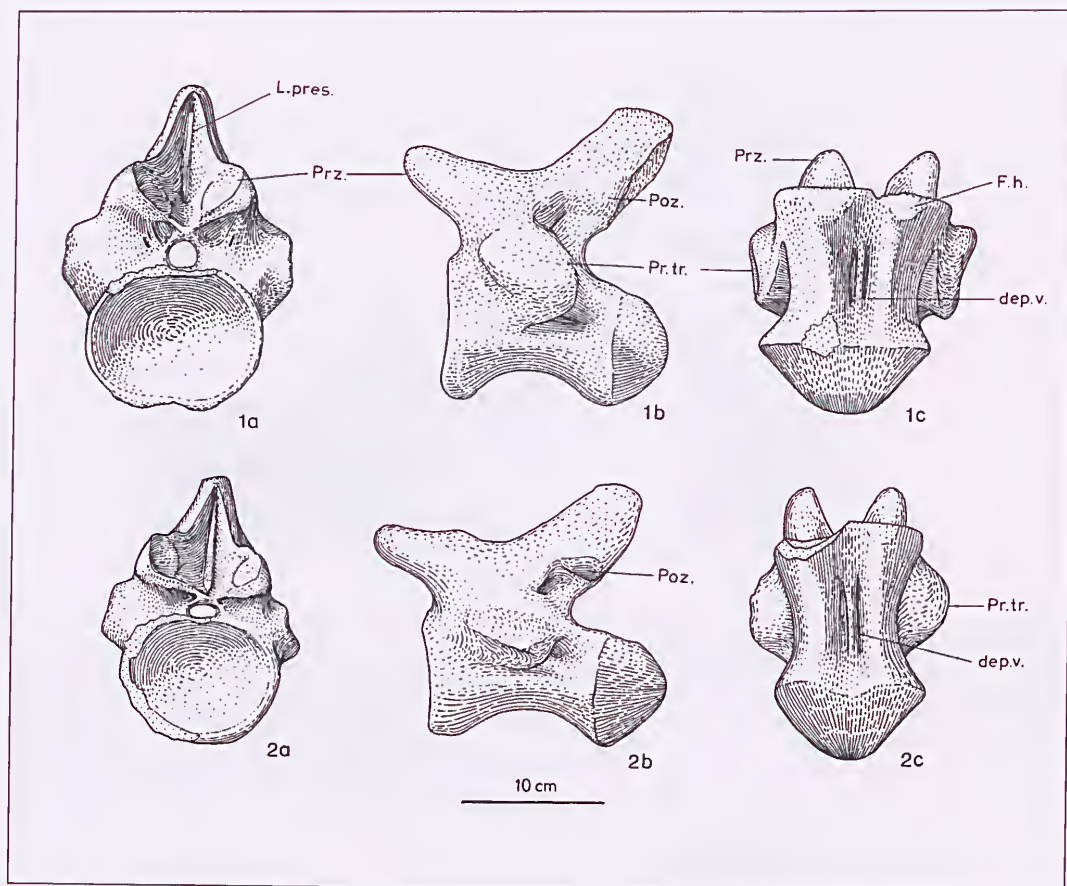


Plate 34. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Caudal vertebra, PVL 4017-28, in (a) anterior, (b) lateral, and (c) ventral views.

2. Caudal vertebra, PVL 4017-33, in (a) anterior, (b) lateral, and (c) ventral views.

Abbreviations. dep. v.: ventral depression; F. h.: facet for the articulation with the hemipophysis; L. pres.: prespinal lamina; Poz.: postzygapophysis; Pr. tr.: transverse process; Prz.: prezygapophysis.

Drawn by E Guanuco.

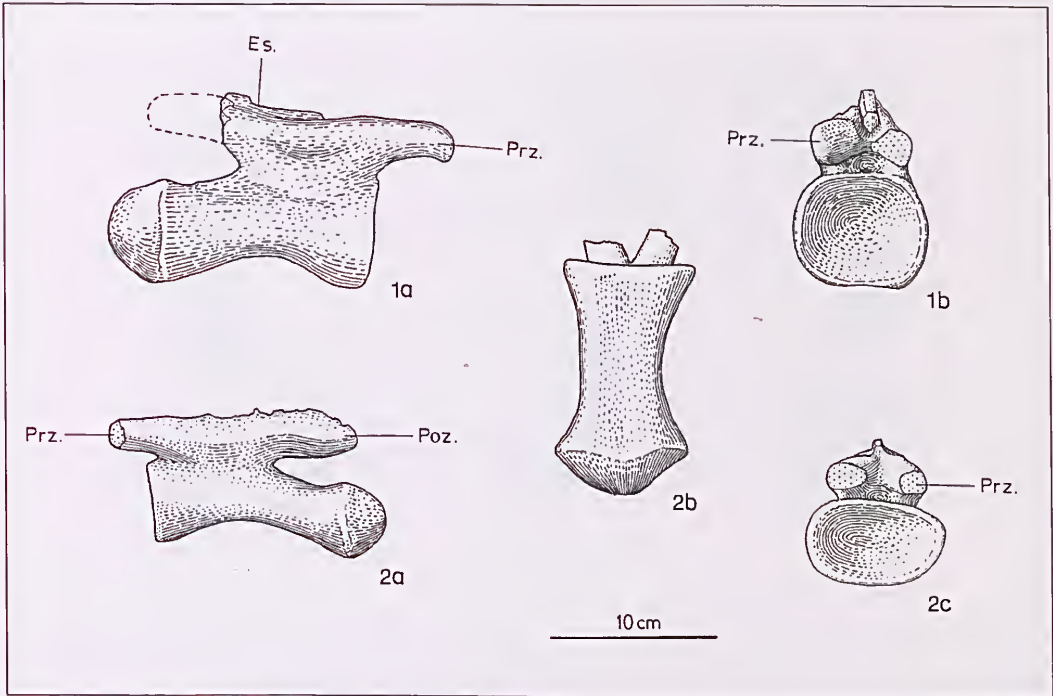


Plate 35. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Distal caudal vertebra, PVL 4017-38, in (a) lateral, and (b) anterior views.

2. Distal caudal vertebra, PVL 4017-39, in (a) lateral, (b) ventral, and (c) anterior views.

Abbreviations. Es.: neural spine; Poz.: postzygapophysis; Prz.: prezygapophysis.

Drawn by E Guanuco.

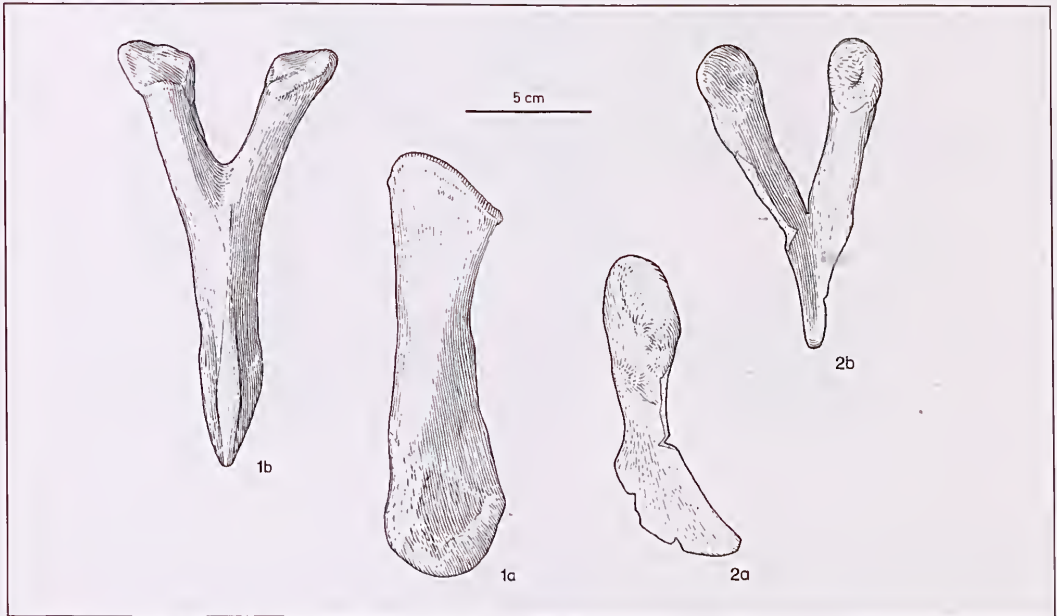


Plate 36. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Anterior hemapophysis, PVL 4017-55, in (a) posterior, and (b) lateral views.

2. Medial hemapophysis, PVL 4017-57, in (a) posterior, and (b) lateral views.

Drawn by E Guanuco.

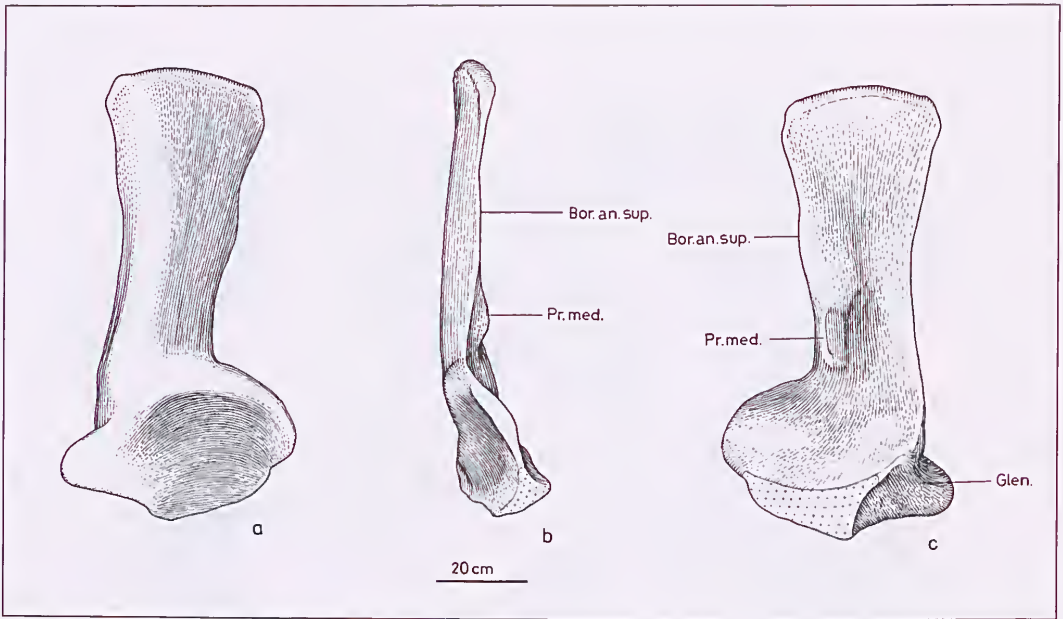


Plate 37. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Right scapula, PVL 4017-106, in (a) lateral, (b) dorsal, and (c) medial views.

Abbreviations. Bor. an. sp.: dorsal anterior border; Glen.: anterior moiety of glenoid fossa; Pr. med.: medial muscular attachment scar.

Drawn by E Guanuco.

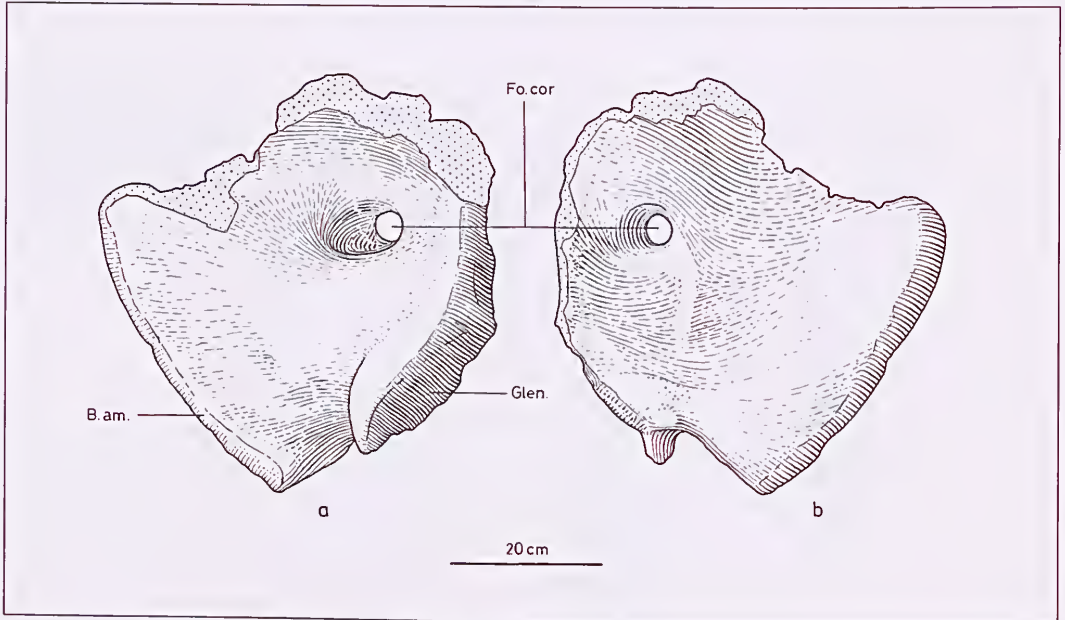


Plate 38. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Left coracoid, PVL 4017-100, in (a) lateral, (b) dorsal, and (c) medial views.

Abbreviations. B. am.: dorsal anteromedial border; Fo. cor.: coracoid foramen; Glen.: coracoid moiety of glenoid fossa.

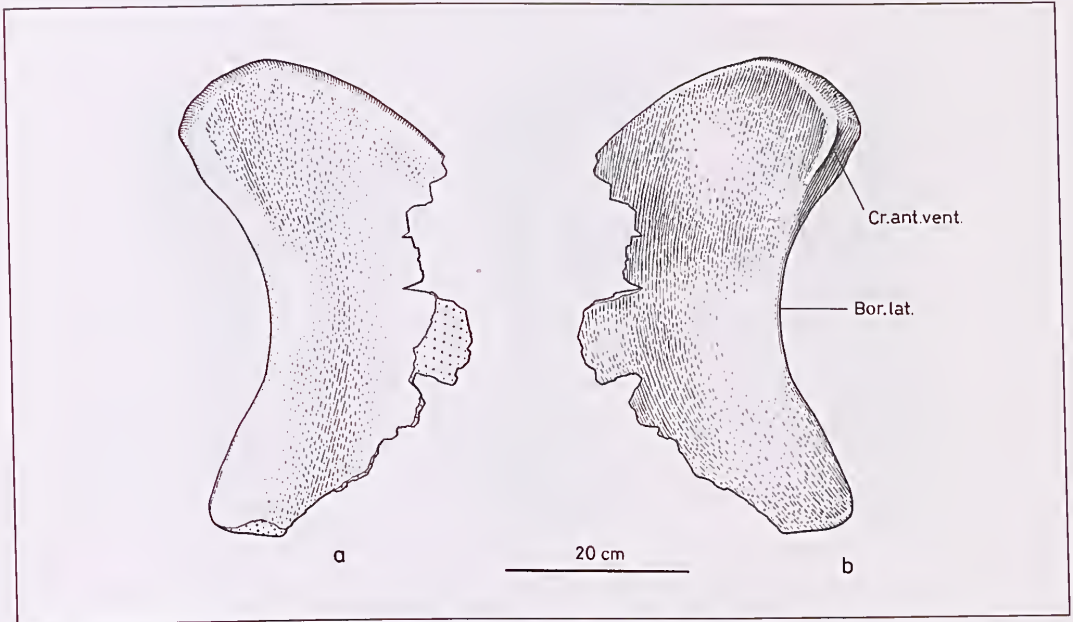


Plate 39. *Saltasaurus loricatus* Bonaparte and Powell 1980.
Left sternal plate, PVL 4017-102, in (a) dorsal and (b) ventral views.
Abbreviations. Cr. ant. vent.: Anteroventral crest; Bor. lat.: lateral border.
Drawn by E Guanuco.

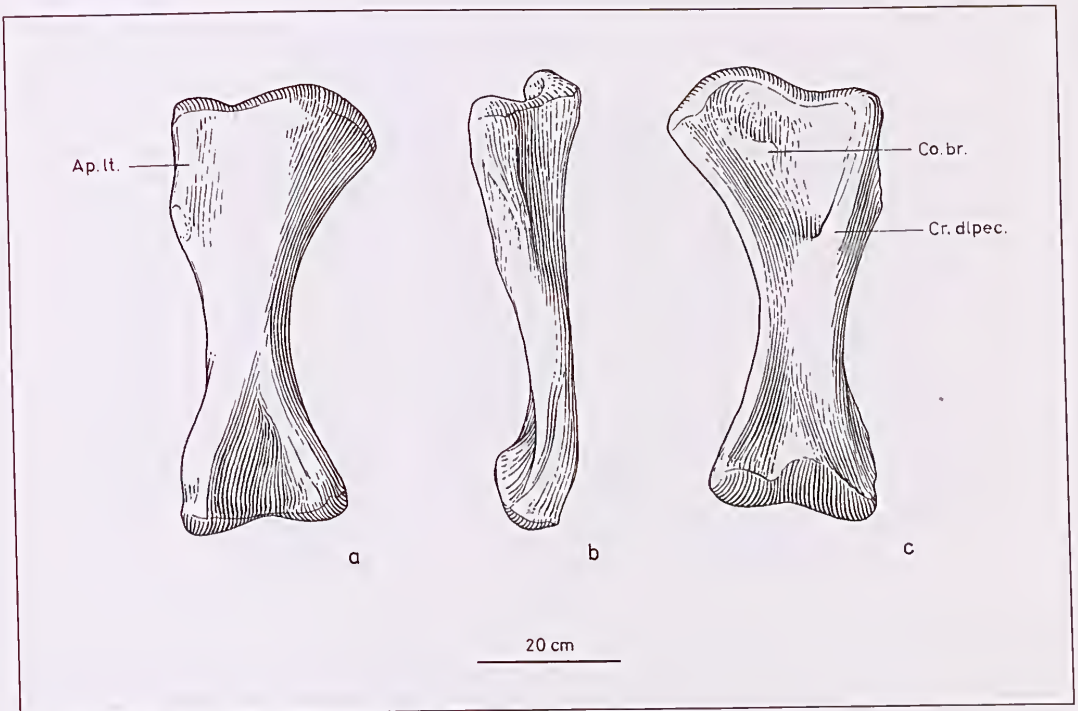


Plate 40. *Saltasaurus loricatus* Bonaparte and Powell 1980.
Left humerus, PVL 4017-67, in (a) posterior, (b) lateral, and (c) anterior views.
Abbreviations. Ap. lt.: lateral apophyses; Co. br.: area of attachment of the coracobrachial muscle; Cr. dipec.: deltopectoral crest.
Drawn by E Guanuco.

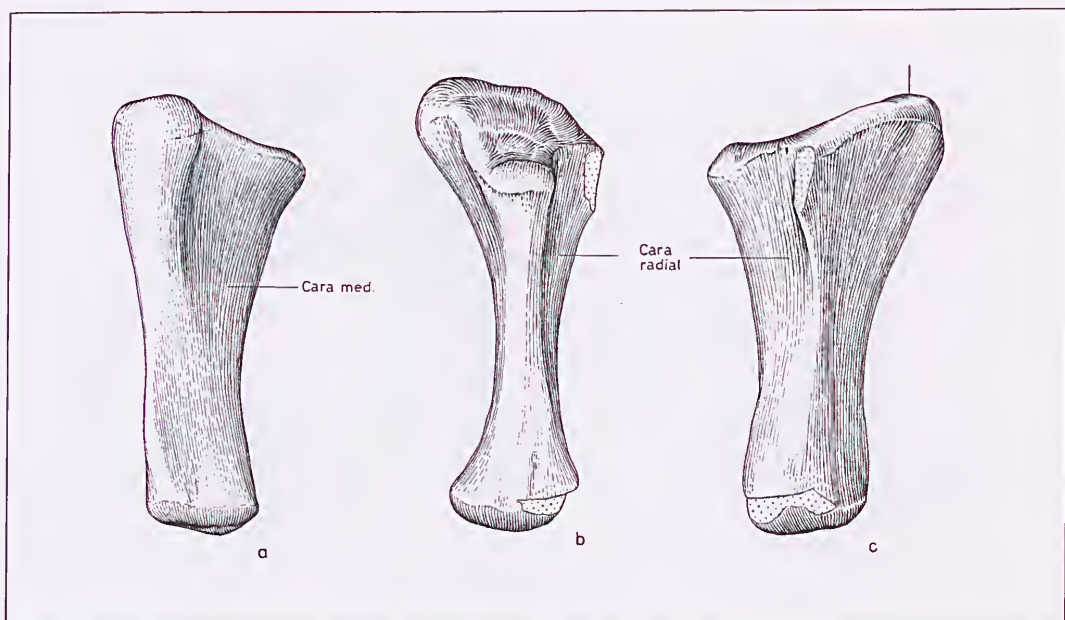


Plate 41. *Saltasaurus loricatus* Bonaparte and Powell 1980.
Left ulna, PVL 4017-74, in (a) medial, (b) anterior, and (c) lateral views.
Abbreviations. Cara med.: medial face; Cara radial: radial face.
Drawn by E Guanuco.

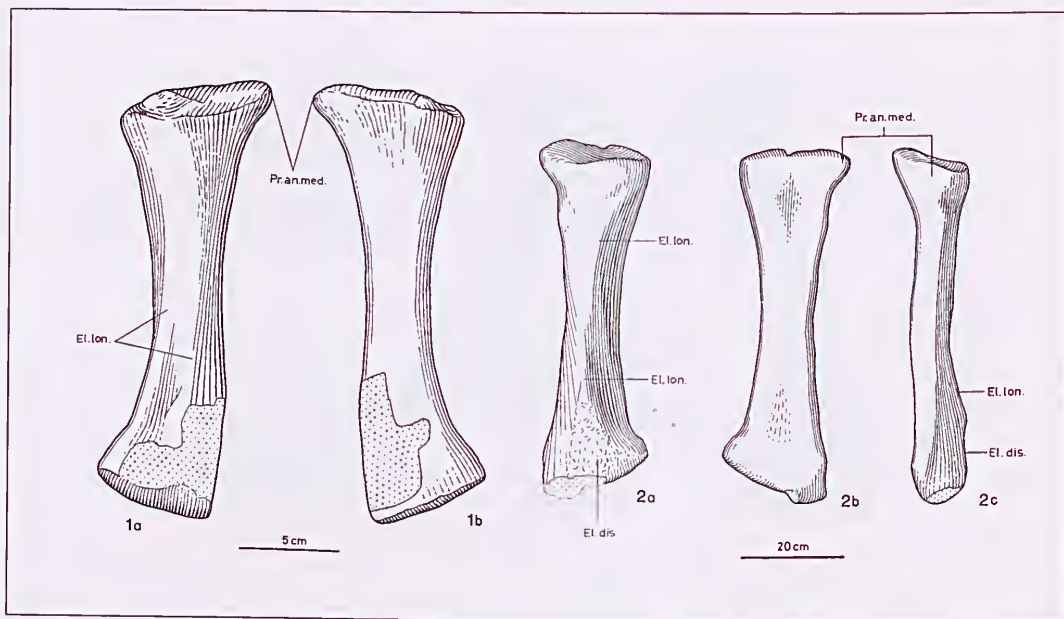


Plate 42. *Saltasaurus loricatus* Bonaparte and Powell 1980.
1. Left radius, PVL 4017-73, in (a) ulnar and (b) anti-ulnar views.
2. Right radius, PVL 4017-79, in (a) ulnar, (b) anti-ulnar, and (c) anteromedial views.
Abbreviations. El. lon.: elongated rugosity; El. dis.: distal rugosity; Pr. an. med.: anteromedial prominence
Drawn by E Guanuco.

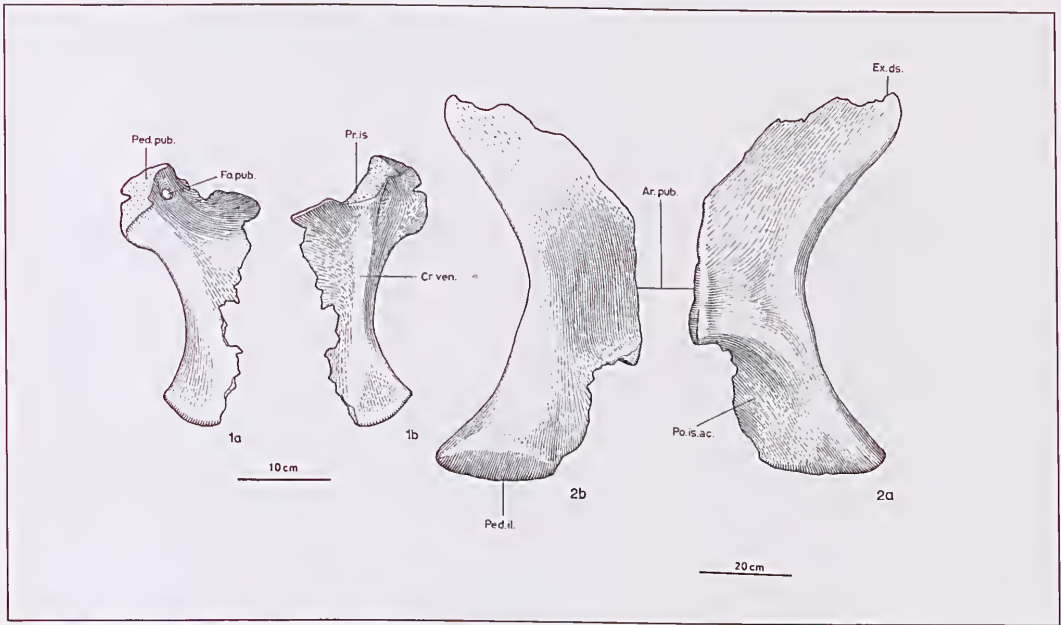


Plate 43. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Right pubis, PVL 4017-95, in (a) dorsal and (b) ventral view.

2. Right ischium, PVL 4017-99, in (a) dorsomedial and (b) ventrolateral views.

Abbreviations. Ar. pub.: area of articulation with the pubis; Cr. ven.: ventral crest; Ex. ds.: distal extremity; Fo. pub.: pubic foramen; ped. il.: iliac peduncle; Ped. pub.: pubic peduncle; Po. is. ac.: ischial moiety of acetabulum; Pr. is.: ischiatic process. Drawn by E Guanuco.

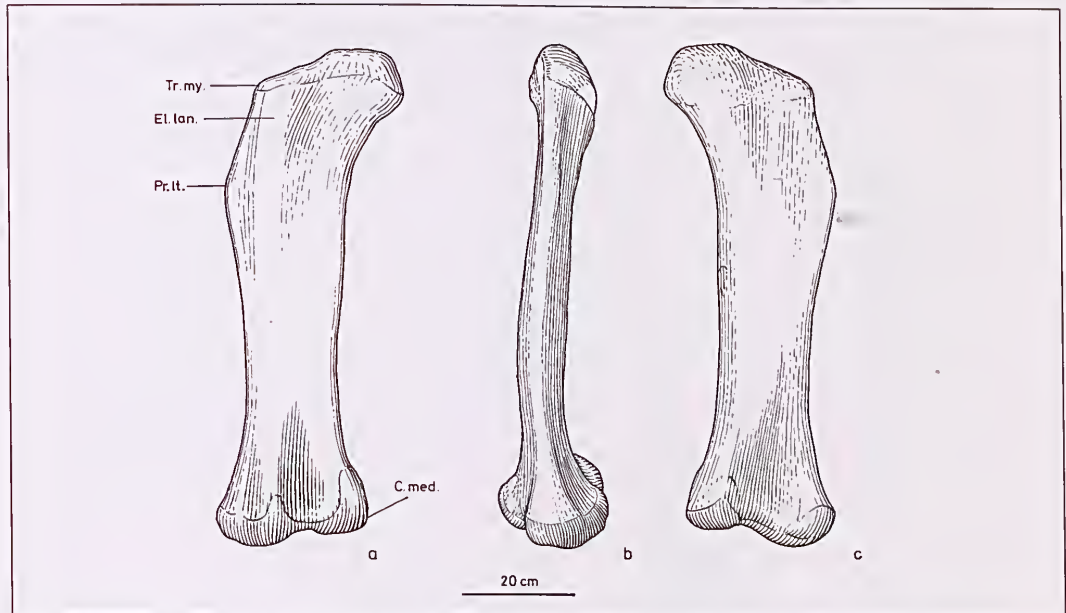


Plate 44. *Saltasaurus loricatus* Bonaparte and Powell 1980.

Right femur, PVL 4017-79, in (a) posterior, (b) lateral, and (c) anterior view.

Abbreviations. C. med.: medial condyle; El. lon.: elongated rugosity; Pr. lt.: lateral prominence of the greater trochanter; Tr. My.: greater trochanter.

Drawn by E Guanuco.

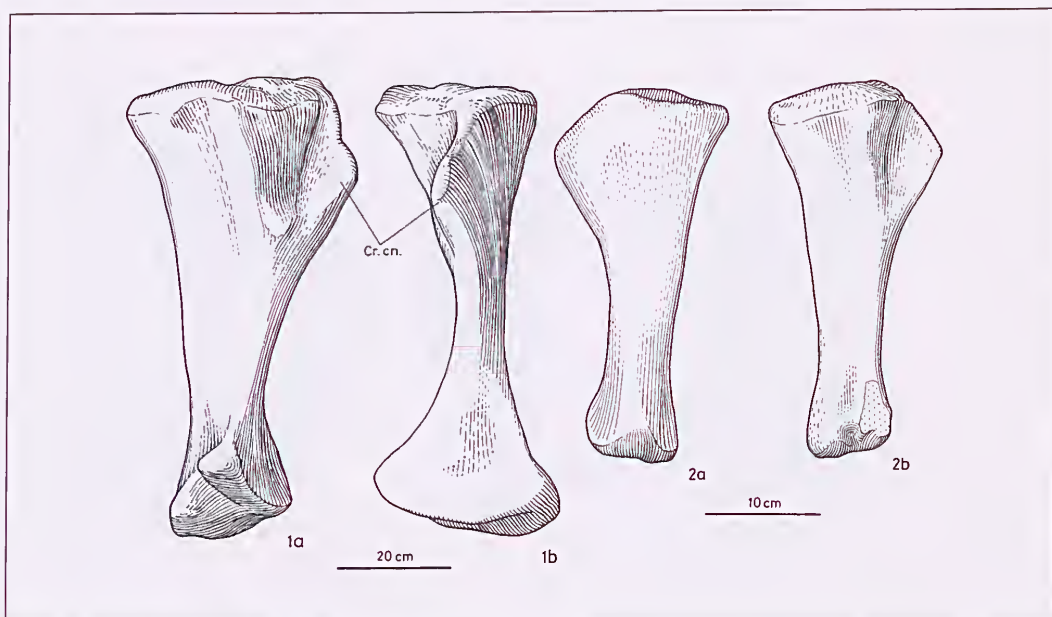


Plate 45. *Saltsaurus loricatus* Bonaparte and Powell 1980.

1. Right tibia, PVL 4017-84, in (a) anterior and (b) lateral view.

2. Juvenile right tibia, PVL 4017-87, in (a) medial and (b) lateral view.

Abbreviation. Cr. cn.: cnemial crest.

Drawn by E Guanuco.

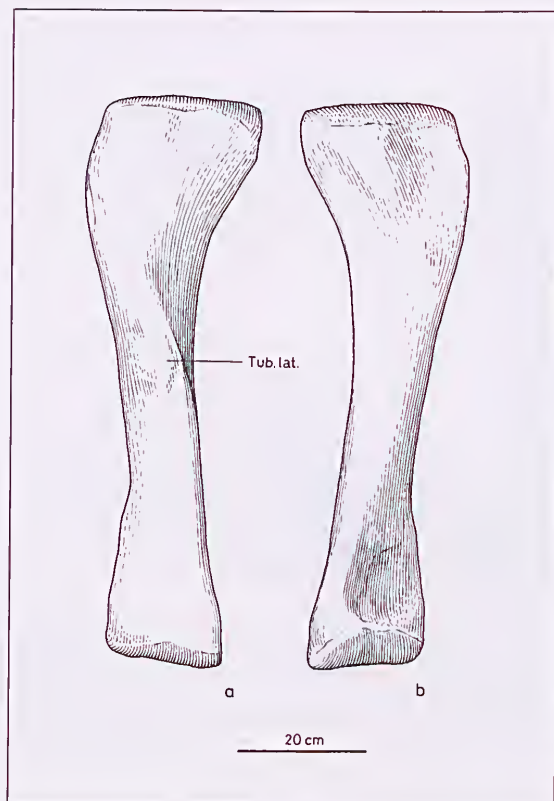


Plate 46. *Saltsaurus loricatus* Bonaparte and Powell 1980.

Left fibula, PVL 4017-87, in (a) lateral and (b) tibial view.

Abbreviation. Tub. lat.: lateral tuberosity.

Drawn by E Guanuco.

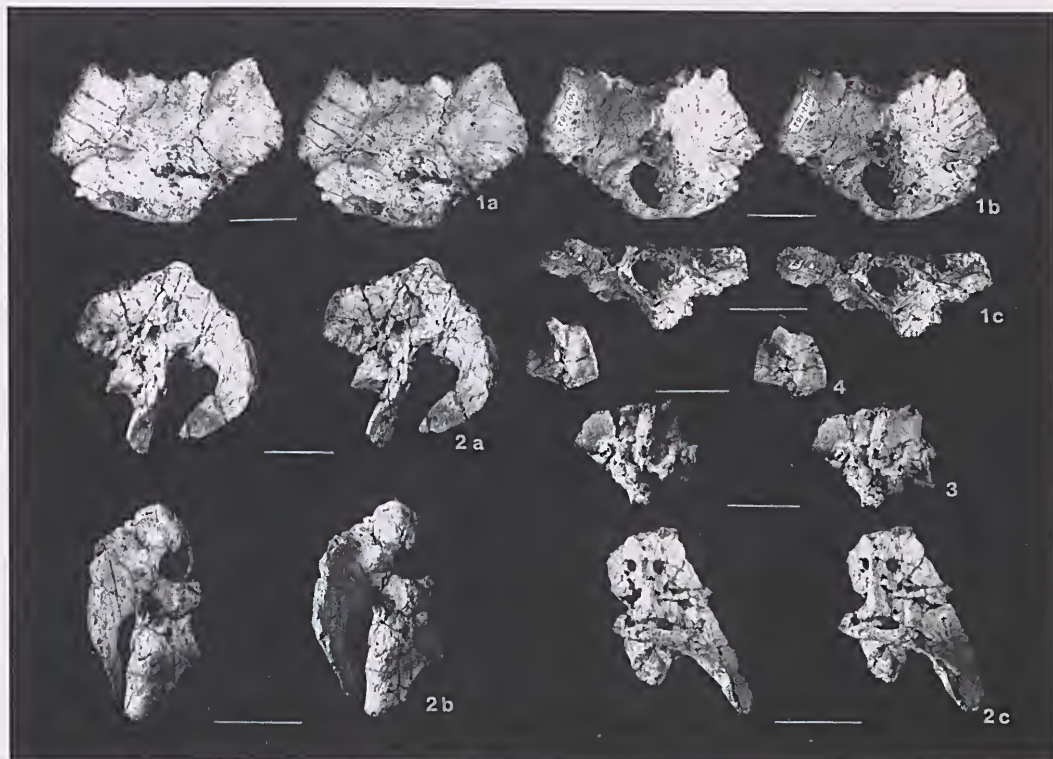


Plate 47. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Juvenile? cranial fragment, PVL 4017-162 in (a) dorsal, (b) ventral, and (c) anterior stereoscopic views.

2. Cranial fragment, PVL 4017-161 in (a) lateral, (b) posterior, and (c) ventral stereoscopic views.

3. Latex endocranial cast made from PVL 4017-161 in lateral stereoscopic view.

4. Juvenile? right frontal, PVL 4017-211, in ventral stereoscopic view.

Scale: 5 cm.

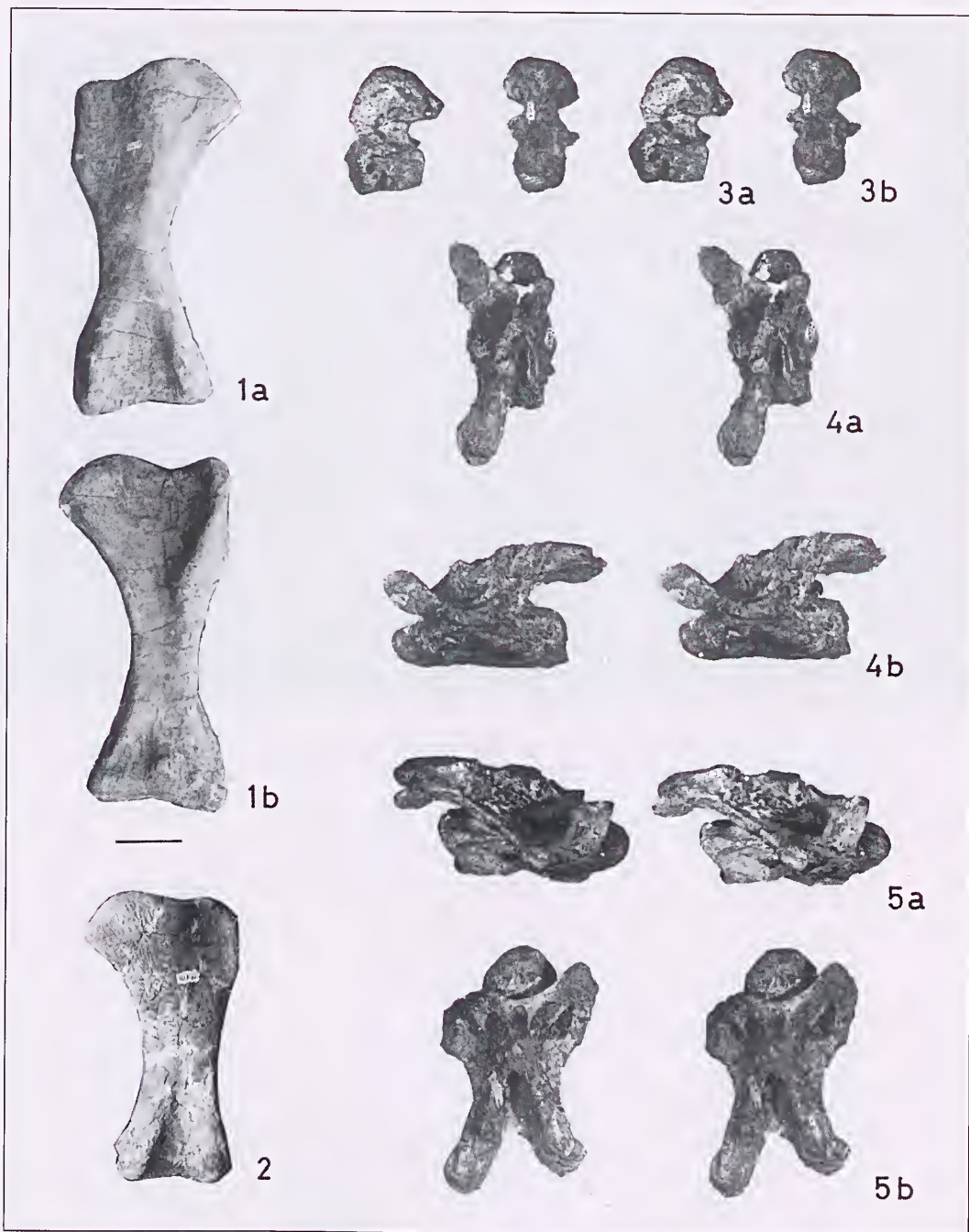


Plate 48. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Left humerus, PVL 4017-67, in (a) posterior and (b) anterior views.

2. Juvenile right humerus, PVL 4017-70 in posterior view.

3. Axis, PVL 4017-1, in (a) lateral and (b) anterior stereoscopic views.

4. Anterior cervical vertebra, PVL 4017-2, in (a) dorsal and (b) lateral stereoscopic views.

5. Mid cervical vertebra, PVL 4017-30, in (a) lateral and (b) dorsal stereoscopic views.

Scale: 10 cm.

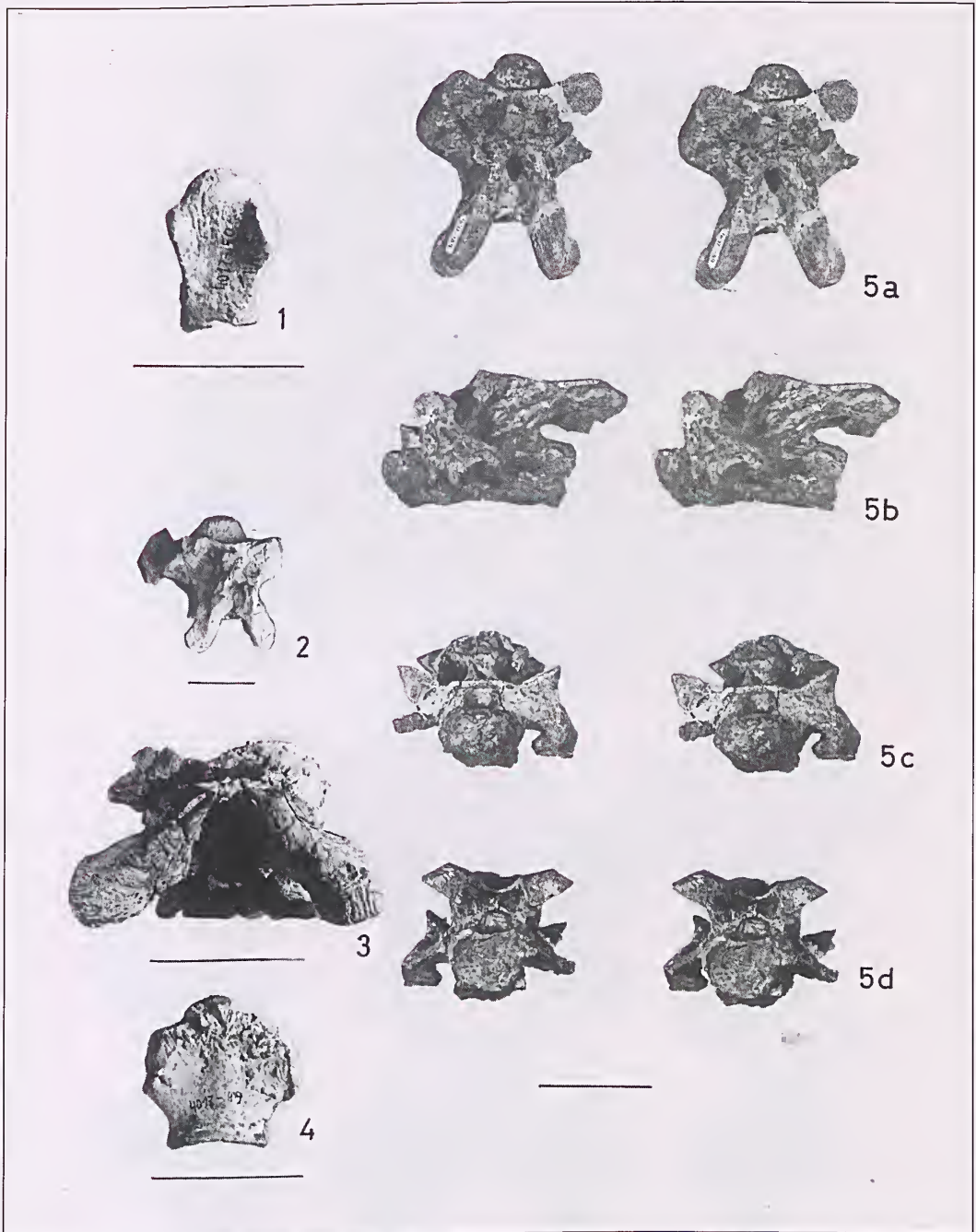


Plate 49. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Centra of juvenile anterior cervical vertebra, PVL 4017-50, in ventral view.
 2. Mid cervical vertebra, PVL 4017-4, in dorsal view.
 3. Posterior cervical vertebra, PVL 4017-8, in posterior view.
 4. Centrum of juvenile posterior cervical vertebra, PVL 4017-49, in ventral view.
 5. Mid cervical vertebra, PVL 4017-139, in (a) dorsal, (b) lateral, (c) anterior, and (d) posterior stereoscopic views.
- Scale: 10 cm.

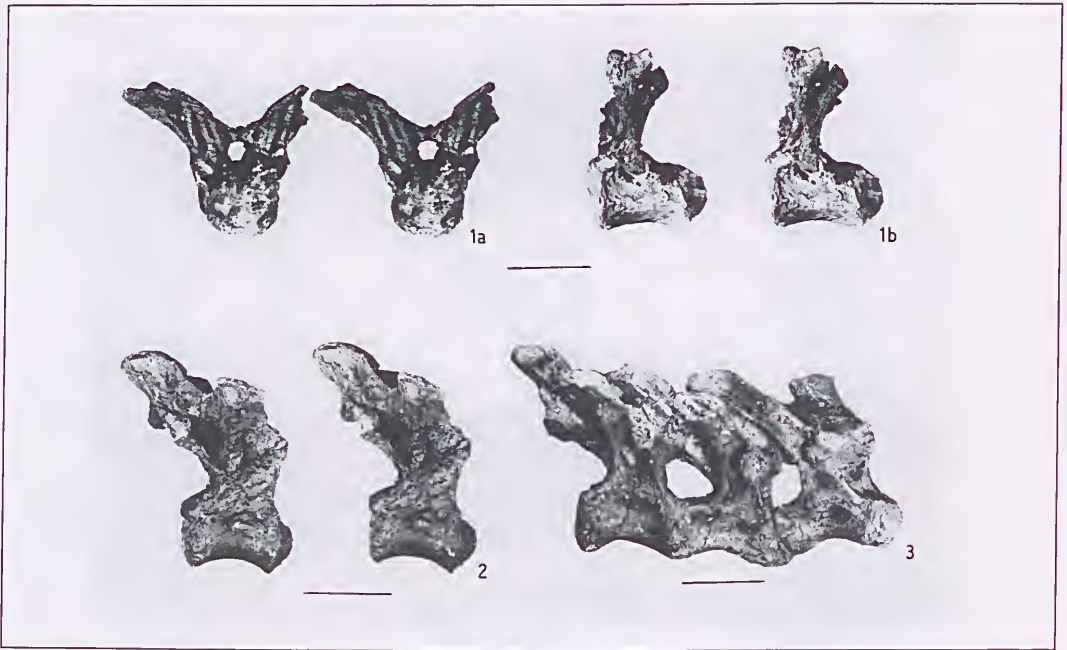


Plate 50. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. First dorsal vertebra, PVL 4017-10, in (a) anterior and (b) lateral stereoscopic views.

2. Posterior dorsal vertebra, PVL 4017-14, in lateral stereoscopic view.

3. Three articulated dorsal vertebra, PVL 4017-42, in lateral view.

Scale: 10 cm.

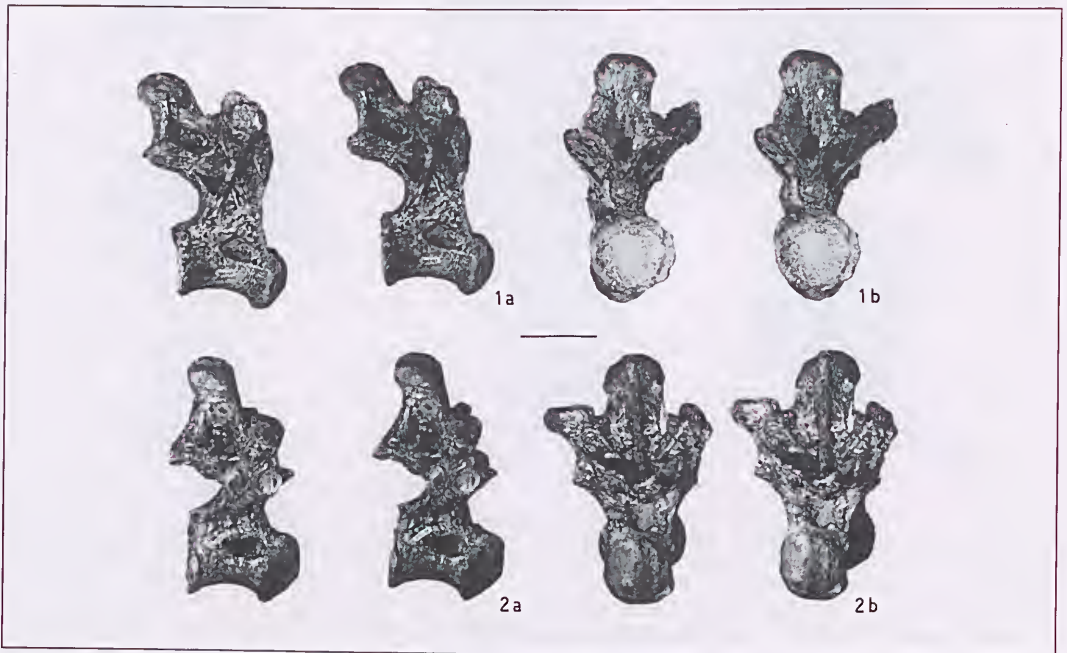


Plate 51. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Eighth? dorsal vertebra, PVL 4017-137, in (a) lateral and (b) posterior stereoscopic views.

2. Tenth? dorsal vertebra, PVL 4017-135, in (a) lateral and (b) anterior stereoscopic views.

Scale: 10 cm.

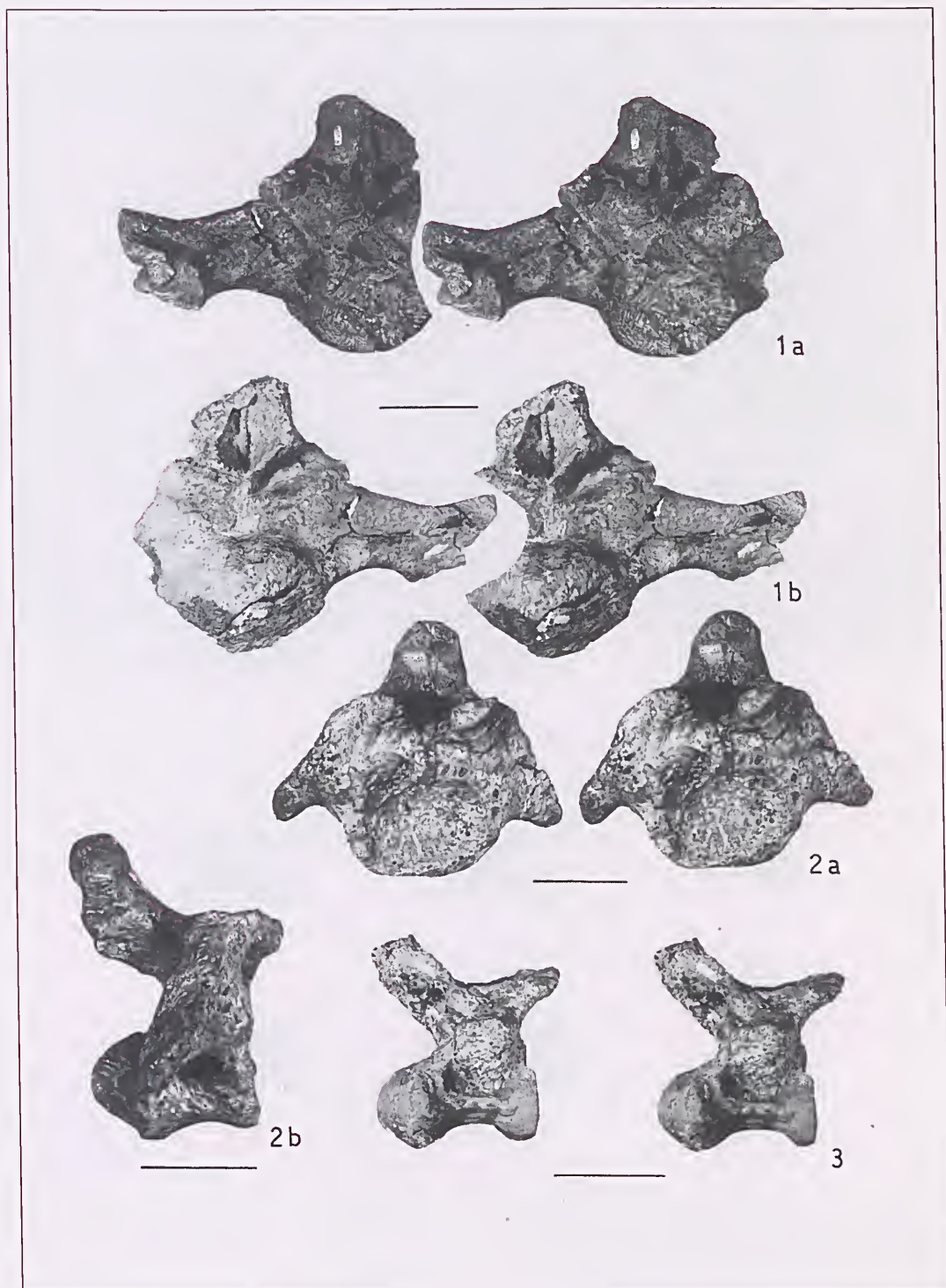


Plate 52. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. First caudal vertebra, PVL 4017-19, in (a) anterior and (b) posterior stereoscopic views.

2. Anterior caudal vertebra, PVL 4017-23, in (a) anterior stereoscopic and (b) lateral monoscopic views.

3. Mid caudal vertebra, PVL 4017-28, in lateral stereoscopic view.

Scale: 10 cm.

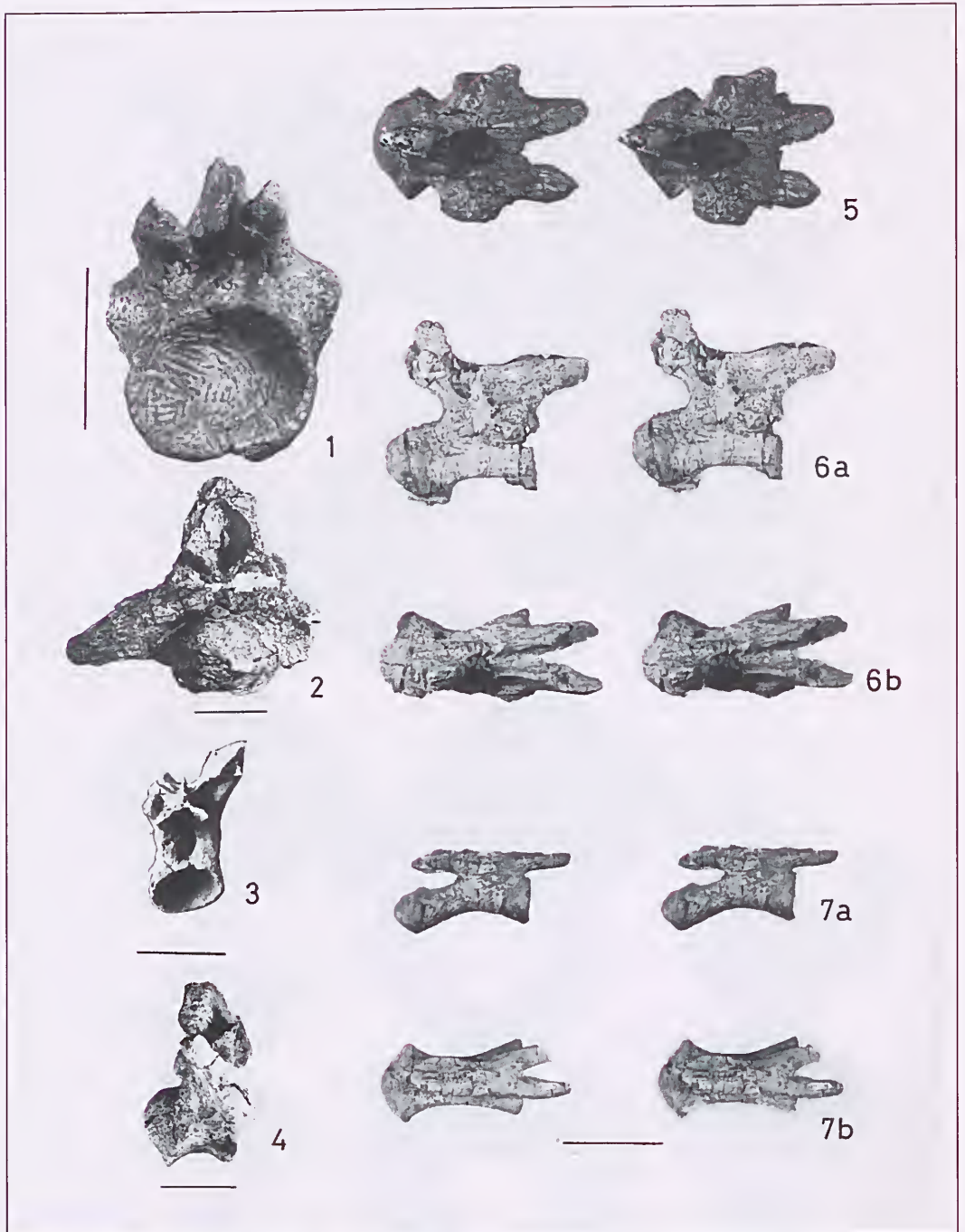


Plate 53. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Mid caudal vertebra, PVL 4017-28, in anterior view.
 2. Anterior caudal vertebra, PVL 4017-21, in posterior view.
 3. Dorsal vertebra showing a section of the neural spine, PVL 4017-14, in posterodorsal view.
 4. Anterior caudal vertebra, PVL 4017-19, in lateral view.
 5. Mid caudal vertebra, PVL 4017-28, in dorsal stereoscopic view.
 6. Mid caudal vertebra, PVL 4017-32, in (a) lateral and (b) dorsal stereoscopic view.
 7. Caudal vertebra, PVL 4017-39, in (a) lateral and (b) dorsal stereoscopic view.
- Scale: 10 cm.

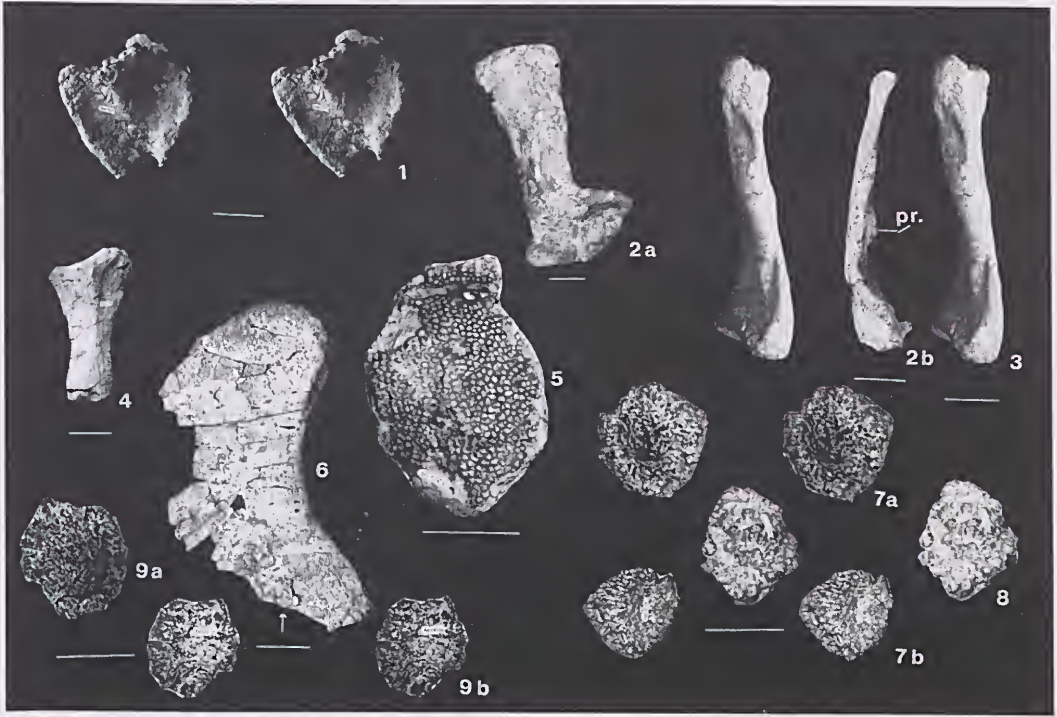


Plate 54. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Left coracoid, PVL 4017-100, in external stereoscopic view.
 2. Right scapula, PVL 4017-106, in (a) lateral and (b) dorsal view.
 3. Left humerus, PVL 4017-67, in lateral stereoscopic view.
 4. Juvenile left ulna, PVL 4017-74.
 5. Conjunction of intradermal bone cells in their original position, PVL 4017-129.
 6. Left sternal plate, PVL 4017-108, in ventral view.
 7. Dermal plate, PVL 4017-112, in (a) external and (b) internal stereoscopic views.
 8. Dermal plate, PVL 4017-113, in external stereoscopic view showing intradermal fusion of the bone cells.
 9. Dermal plate, PVL 4017-134 in (a) external view and (b) internal stereoscopic view.
- Abbreviation. Pr.: process for muscular attachment.
Scale: 10 cm.



Plate 55. *Saltsaurus loricatus* Bonaparte and Powell 1980.

1. Left femur, PVL 4017-79, in (a) posterior, (b) anterior, and (c) medial views.
 2. Left tibia, PVL 4017-88, in fibular view.
 3. Fibula, PVL 4017-89, in (a) lateral and (b) medial views.
 4. Tibia, PVL 4017-84, in fibular view.
 5. Juvenile tibia, PVL 4017-87, in fibular view.
 6. Sacrum articulated with both ilia, PVL 4017-93, in (a) lateral and (b) posterodorsal view.
 7. Sacrum articulated with right ilium and partial left ilium, PVL 4017-92 (holotype) in (a) dorsal and (b) posterior view.
 8. Incomplete sacrum, PVL 4017-18, in ventral view.
 9. Right pubis, PVL 4017-95, in ventral view.
 10. Right ischium, PVL 4017-99, in dorsomedial view.
- Scale: 10 cm.



Plate 56. *Neuquensaurus australis* (Lydekker 1893)

1. Second? dorsal vertebra, MCP CS 1373, in (a) anterior, (b) dorsal, and (c) posterior stereoscopic views.

2. Posterior most? cervical vertebra, MCP CS 1376, in (a) posterior, (b) anterior, and (c) dorsal views.

3. Eleventh? cervical vertebra, MCP CS 1374, in (a) anterior, (b) posterior, and (c) dorsal views.

Scale: 10 cm.

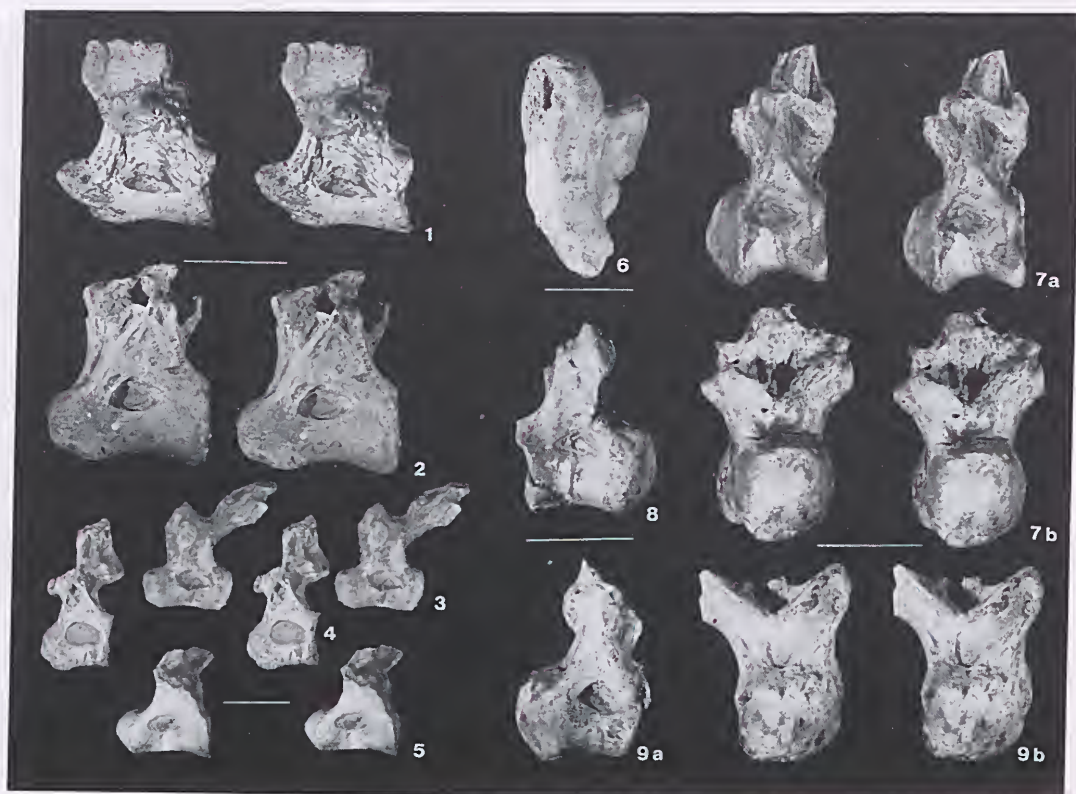


Plate 57. *Neuquensaurus australis* (Lydekker 1893)

1. Anterior dorsal vertebra, third?, MLP CS 1379, in lateral stereoscopic view.
2. Posterior dorsal vertebra, MLP CS 1382, in lateral stereoscopic view.
3. Fourth? dorsal vertebra, MLP CS 1381, in lateral stereoscopic view.
4. Posterior dorsal vertebra in lateral stereoscopic view.
5. Fifth? dorsal vertebra, MLP '30', in lateral stereoscopic view.
6. Partial anterior dorsal vertebra, MLP 126 150, in ventral view.
7. Tenth? dorsal vertebra, MLP CS 1367, in (a) lateral and (b) anterior stereoscopic views.
8. Posterior dorsal vertebra in lateral view.
9. Tenth? dorsal vertebra, MLP CS 1386, in (a) lateral and (b) anterior views.

Scale: 10 cm.

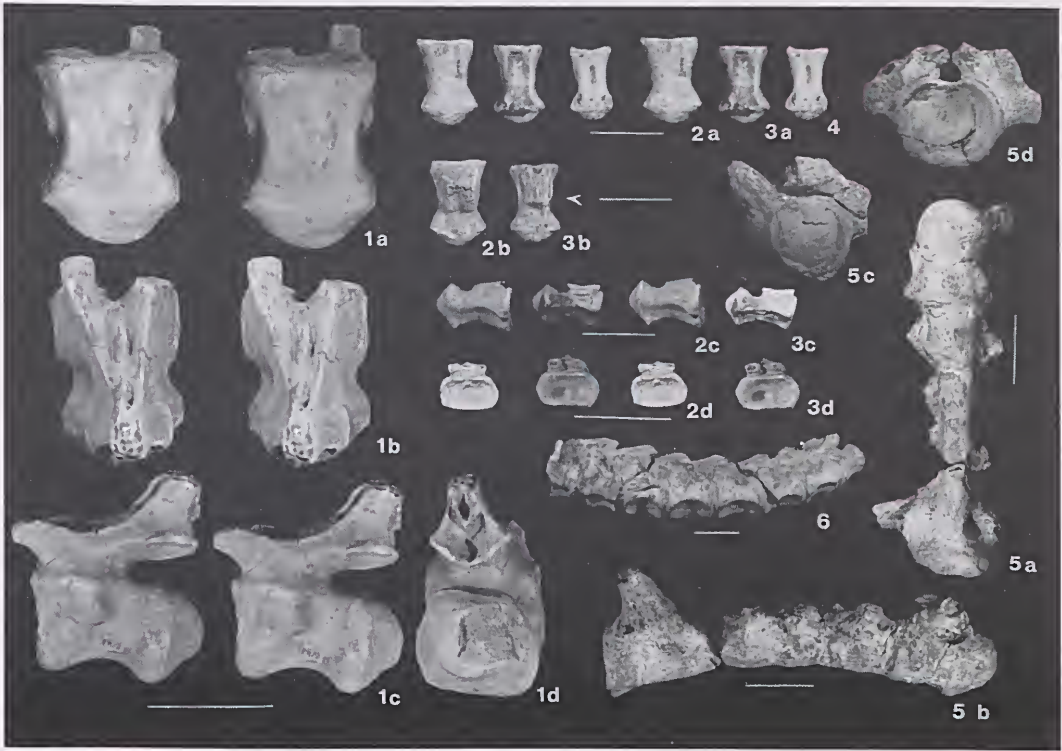


Plate 58. *Neuquensaurus australis* (Lydekker 1893)

1. Medial caudal vertebra, MLP CS 1413, in (a) ventral, (b) dorsal, and (c) lateral stereoscopic views and (d) posterior monoscopic view.
 2. Distal caudal vertebra in (a) lateral, (b) dorsal, (c) ventrolateral, and (d) anterior stereoscopic views.
 3. Distal caudal vertebra in (a) ventral stereoscopic view, (b) dorsal monoscopic view, and (c) ventrolateral and (d) anterior stereoscopic views.
 4. Distal caudal vertebra in ventral stereoscopic view.
 5. Sacrum, MLP Ly 7, in (a) dorsal, (b) lateral, (c) anterior, and anterior caudal vertebra, MLP CS Ly 8, (d) posterior views.
 6. Eighth caudal vertebrae, MLP CS 1408, 1409 and 1410, in lateroventral view.
- Scale: 10 cm.



Plate 59. *Neuquensaurus australis* (Lydekker 1893)

1. Right humerus, MLP CS 1099, in (a) anterior and (b) posterior views.

Neuquensaurus robustus (Huene 1929a) *nomen dubium*

2. Left ulna, MLP CS 1052, in radial view.

3. Right radius, MLP CS 1169, in ulnar stereoscopic view.

Neuquensaurus australis (Lydekker 1893)

4. Left scapula and coracoid, MLP CS 1096, in external view.

5. Right ulna, MLP CS 1095, in radial view.

Neuquensaurus robustus (Huene 1929a) *nomen dubium*

6. Right ulna, MLP CS 1094, in caudal view.

7. Left radius, MLP 1176, in ulnar view.

Scale: 10 cm.

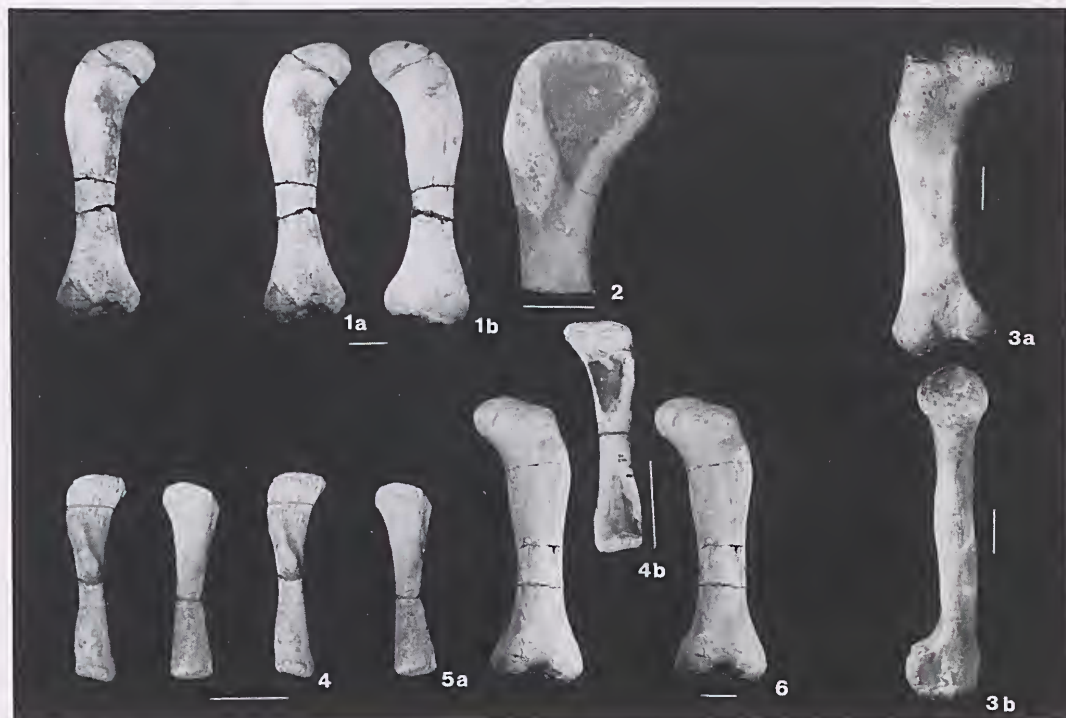


Plate 60. cf. *Titanosaurus* sp.

1. Right femur in (a) anterior stereoscopic view and (b) posterior monoscopic view, MLP CS 1122. This specimen was assigned to '*Titanosaurus australis*' in Huene (1929a).

Neuquensaurus robustus (Huene 1929a) *nomen dubium*

2. Proximal moiety of the right humerus, MLP CS 1019, in anterior view.

3. Left femur, MLP CS 1480, in (a) anterior and (b) medial view.

4. Left fibula, MLP CS 1265, in lateral view.

Neuquensaurus australis (Lydekker 1893)

5. Right fibula, MLP CS 127, in lateral view.

6. Left femur, MLP CS 1118, in anterior stereoscopic views.

Scale: 10 cm.

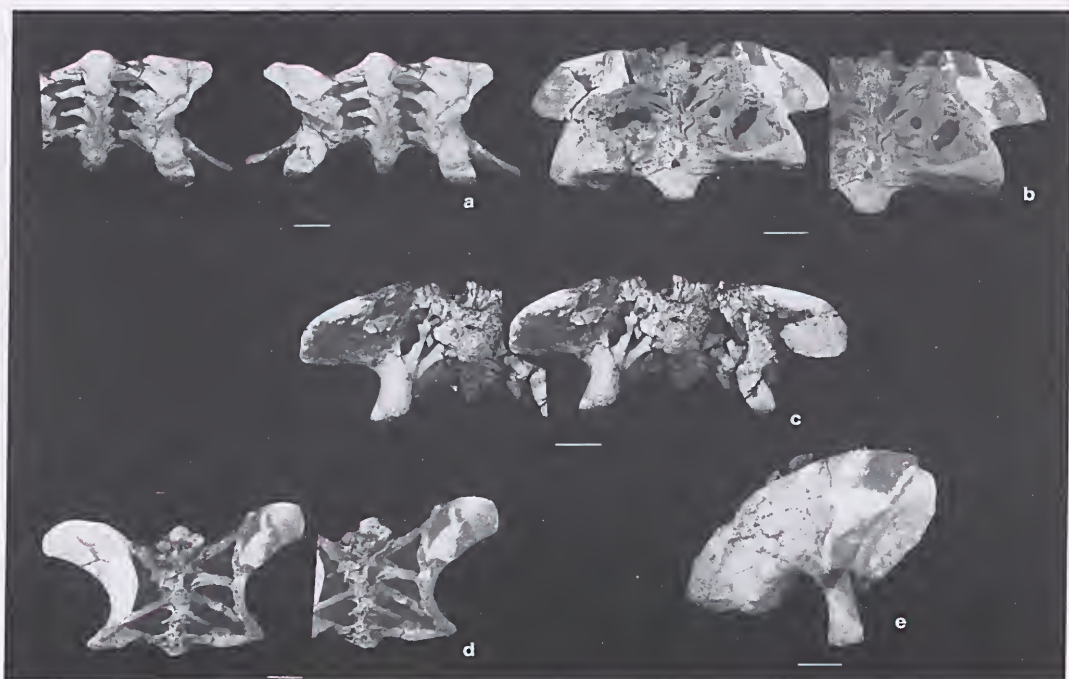


Plate 61. Titanosauridae indet.

Sacrum fused to the two ilia in (a) posteroventral, (b) posterodorsal, (c) anterior, (d) dorsal stereoscopic views and (e) right antero-lateral in monoscopic view. [Editor's note: registration numbers not ascertainable for specimens illustrated in Pl. 61.]

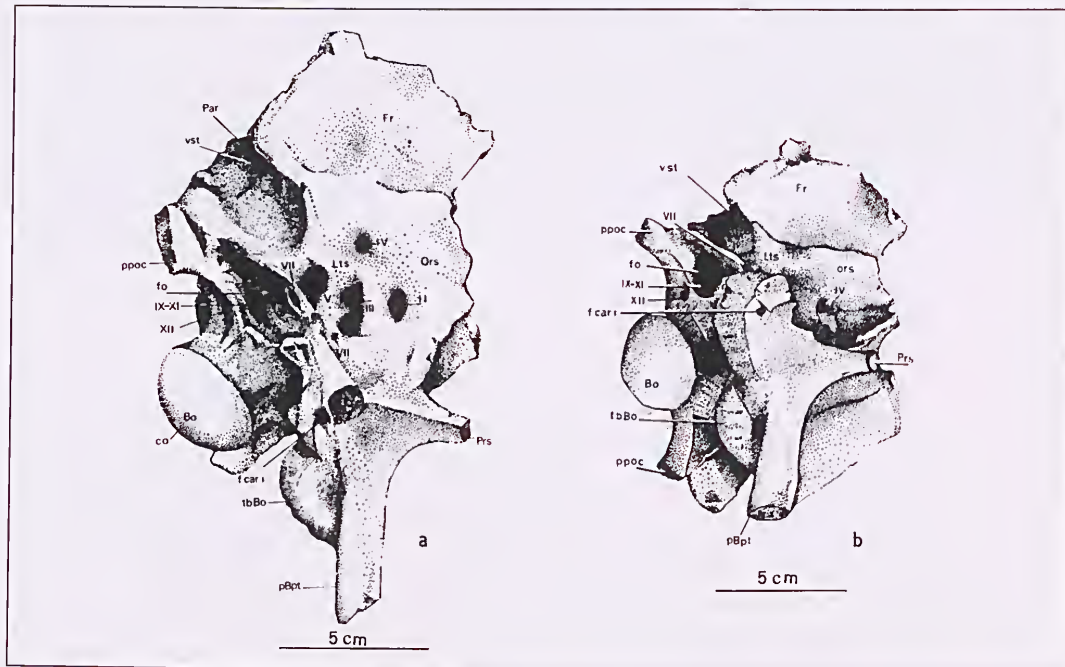


Plate 62. *Antarctosaurus wichmannianus* Huene 1929a.

Fragment of skull, MACN 6904, in (a) lateroventral and (b) ventral views.

Abbreviations. Bo.: basioccipital; c.o.: occipital condyle; f. car. i.: internal carotid foramen; fo.: fenestra ovalis; Fr.: frontal; Lts.: laterosphenoid; Ors. [=ors.]: orbitosphenoid; Par.: parietal; pBpt.: basipterygoid process; ppoc.: paroccipital process; Prs.: presphenoid; tbBo.: basal tuberosity of the basioccipital; vst.: supratemporal fenestra.

Drawn by A Castillo.

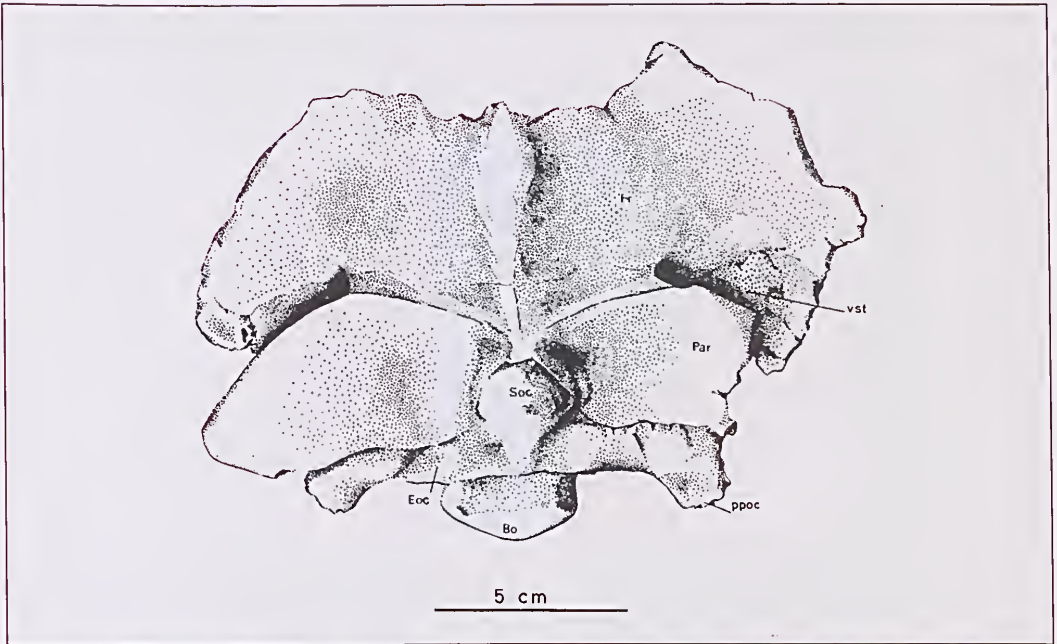


Plate 63. *Antarctosaurus wichmannianus* Huene 1929a.

Fragment of skull, MACN 6904, in dorsal view.

Abbreviations. Bo.: basioccipital; Eoc.: exoccipital; Fr.: frontal; Par.: parietal; ppoc.: paroccipital process; Soc.: supraoccipital; vst.: supratemporal fenestra.

Drawn by A Castillo.

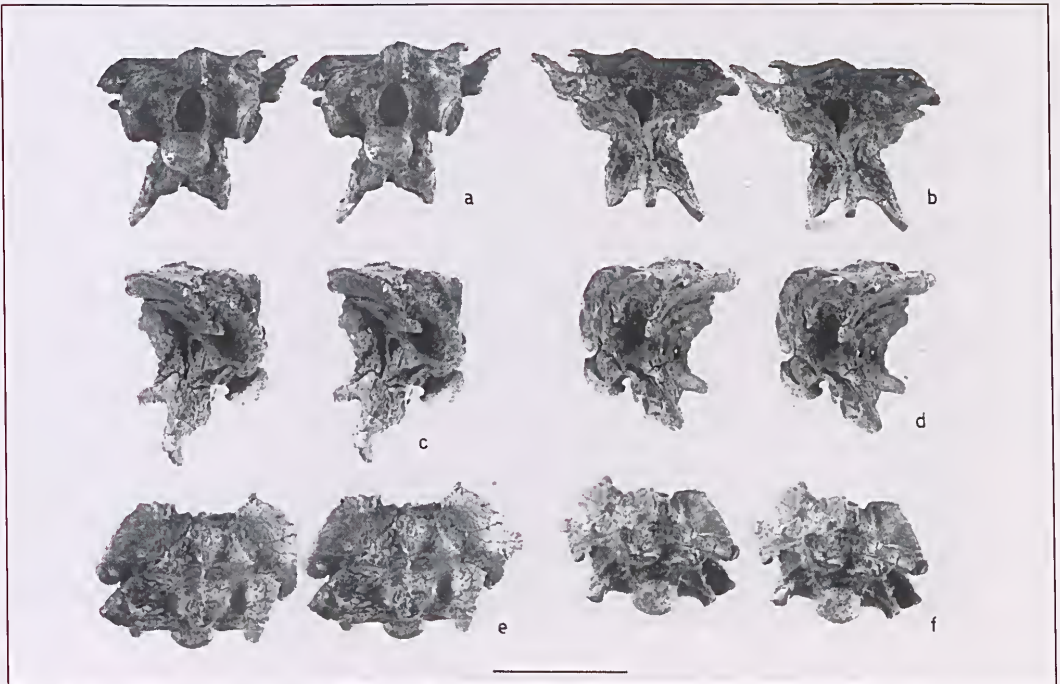


Plate 64. *Antarctosaurus wichmannianus* Huene 1929a.

Fragment of skull, MACN 6904, in (a) posterior, (b) anterior, (c) left lateral, (d) right lateral, (e) dorsal, and (f) ventral stereoscopic views.

Scale: 10 cm.



Plate 65. *Sphaerovum erbeni* Mones 1980

1. Cross section of fragment of pathological eggshell showing three distinct shell layers, MNHN – DP 713.
2. Detailed illustration of the external surface of a shell showing its texture.
3. Complete fossil eggshell, MNHN – DP 713.
4. Complete fossil eggshell, MMAB.

Indeterminate titanosaurs

5. Caudal vertebra of Titanosauridae indet., MMAB
6. Caudal vertebra of Titanosaurinae indet., MMAB 250, in anterior view.
7. Caudal vertebra of Titanosaurinae indet., MMAB 250, in lateral view.
8. Anterior caudal vertebra, MMAB 4073, in lateral view.
9. Distal anterior caudal vertebra, MMAB 3143, in lateral view.
10. Anterior moiety of titanosaur sacrum, MNHN

Antarctosaurus wichmannianus Huene 1929a

11. First caudal vertebra, MACN 6904, in (a) lateral, (b) posterior, and (c) anterior views.
12. Left femur, MACN 6904, in (a) posterior and (b) distal views.
13. (upper image) Left fibula, MACN 6904, in lateral view.
13. (lower image) Scapula, MACN 6904, in lateral view.

Scale: 10 cm.

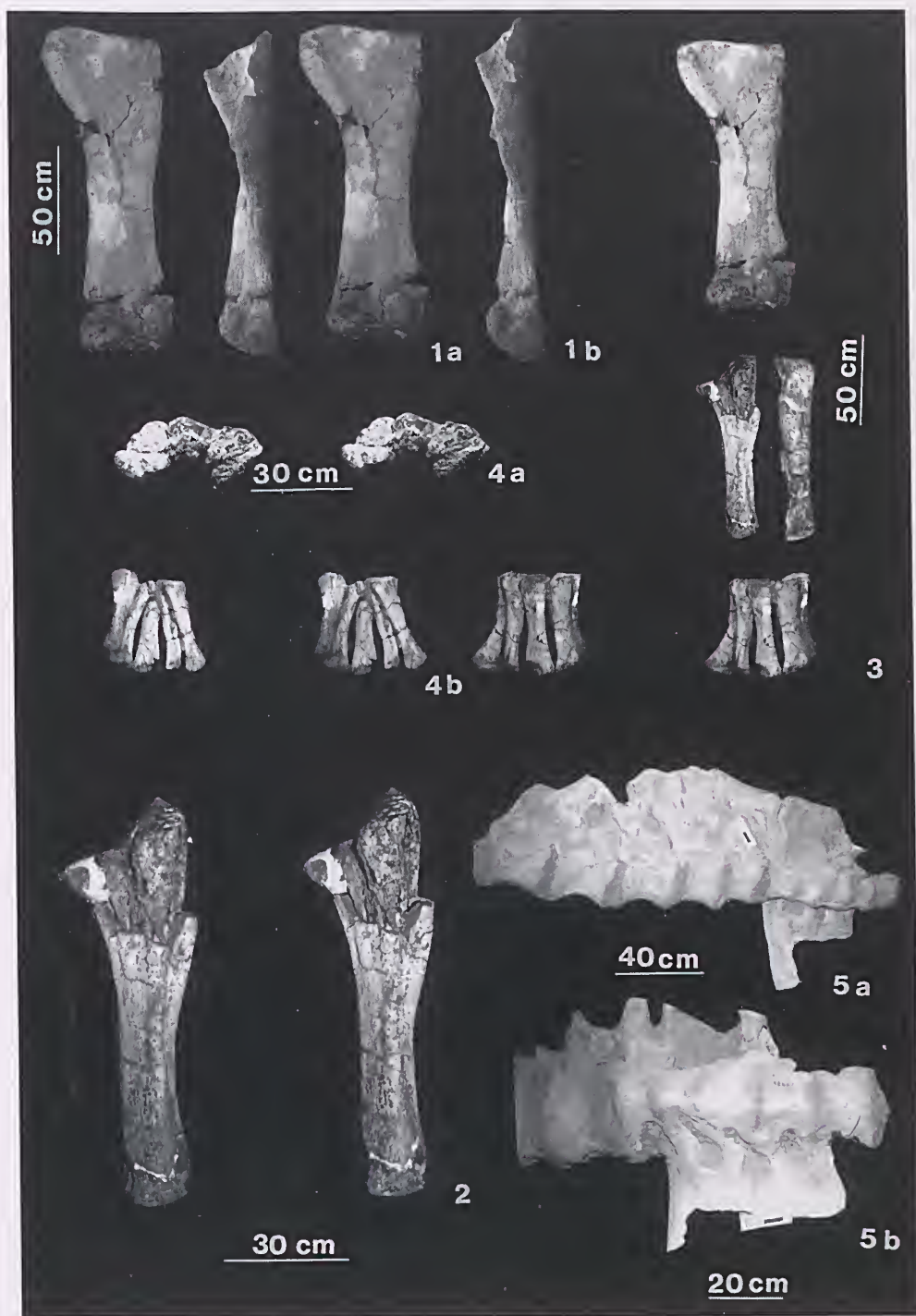


Plate 66. *Argysaurus superbus* Lydekker 1893 (holotype)

1. Left humerus in (a) anterior and (b) lateral stereoscopic views.

2. Left ulna in radial stereoscopic view.

3. Left humerus, ulna, radius, and metacarpals at the same scale.

4. Articular metacarpals in (a) proximal and (b) palmar stereoscopic views.

Epachthosaurus sciuttoi gen. et sp. nov. (paraplastotype)

5. (a) Posterior dorsal vertebrae and sacrum in lateroventral view and (b) sacrum and posterior most dorsal vertebra in ventral view.

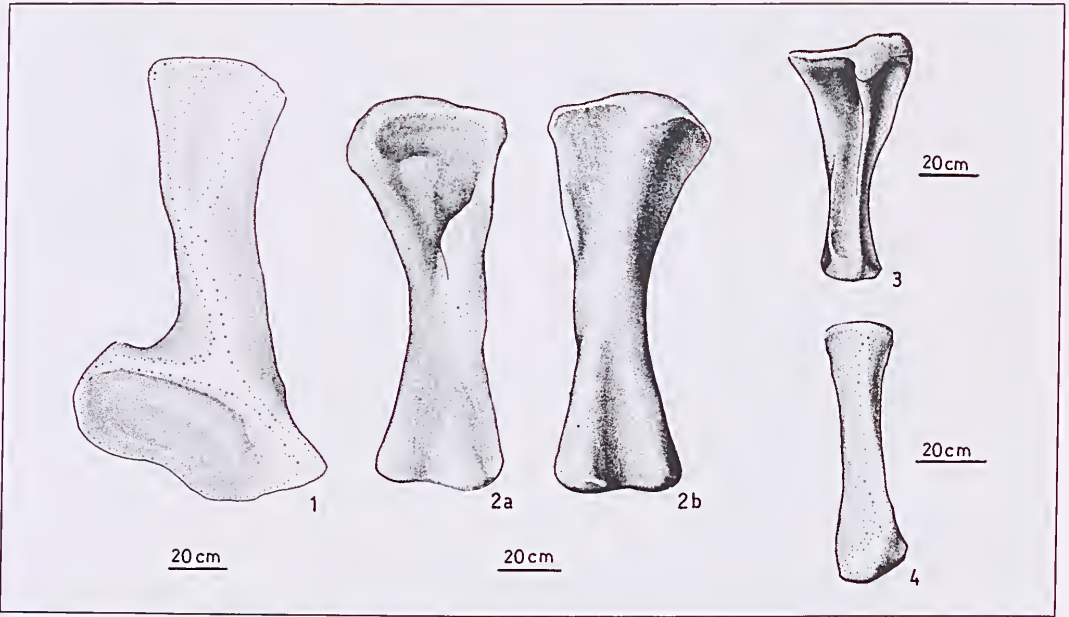


Plate 67. *Argyrosaurus superbus?*, PVL 4628.

1. Left scapula in lateral view.
2. Left humerus in (a) anterior and (b) posterior views.
3. Left ulna in radial view.
4. Left radius.

Drawn by E Guanuco.

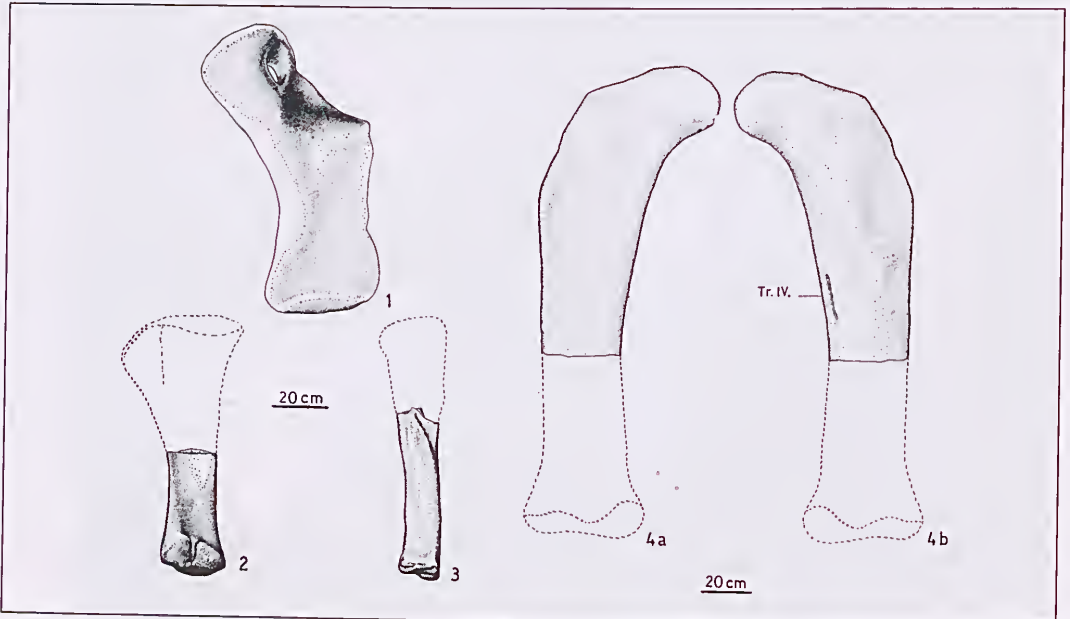


Plate 68. *Argyrosaurus superbus?*, PVL 4628.

1. Right pubis in dorsal view.
2. Left ulna in fibular view.
3. Fibula in lateral view.
4. Right femur in (a) anterior and (b) posterior view.

Abbreviation. Tr. IV.: fourth trochanter

Drawn by E Guanuco.



Plate 69. *Argysaurus superbus?*, PVL 4628.

1. Posterior dorsal vertebra in lateral view.

2. Posterior dorsal vertebra in (a) anterior and (b) lateral view.

3. Medial dorsal vertebra in lateral view.

4. Anterior caudal vertebra in (a) posterior stereoscopic view, and (b) lateral and (c) anterior monoscopic views.

5. Left scapula in lateral view.

6. Dorsal rib.

Scale: 10 cm.



Plate 70. Cf. *Argyrosaurus* sp.

1. Right femur, FMNH 13018, in anterior view.

2. Right femur, FMNH 13019, in anterior view.

3. Left tibia, FMNH P 13020, in lateral view.

Argyrosaurus superbus? PVL 4628

4. Right pubis in dorsal view.

5. Proximal half of right femur in anterior view.

6. Right humerus in lateral view.

7. Right ulna and radius in anterior stereoscopic view.

Argyrosaurinae?

8. Right femur in anterior view.

9. Incomplete cervical vertebra, Col. MACN, from Lake Argentina in lateral view.

10. Distal caudal vertebra in (a) posterior, (b) ventral, and (c) lateral stereoscopic view.

[Editor's note: registration numbers not ascertainable for specimens illustrated in Pl. 70:8, 10.]

Scale: 10 cm.

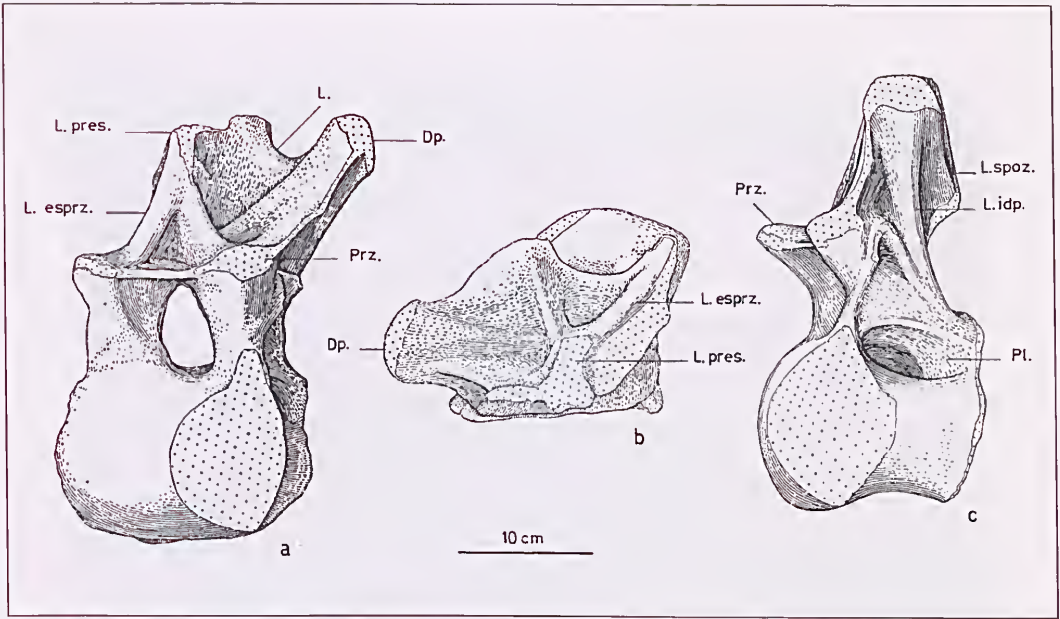


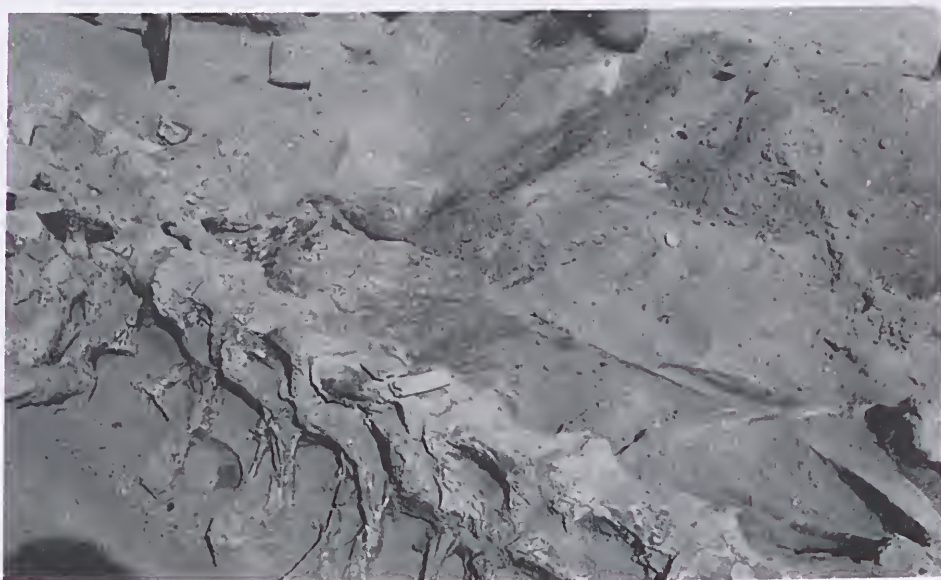
Plate 71. *Epachthosaurus sciuttoii* gen. et sp. nov.

Posterior dorsal vertebra in (a) anterior, (b) dorsal, and (c) lateral view.

Abbreviations. Dp.: dorsal process; L.: lamina; L. esprz.: spinal-prezygapophyseal lamina; L. idp.: infradiapophyseal lamina; L. pres.: prespinal lamina; L. spoz.: suprapostzygapophyseal lamina; Pl.: pleurocoel; Prz.: prezygapophysis.



a



b

Plate 72. *Pellegrinisaurus powelli* Salgado 1996

a. View of the dorsal region of the articulated vertebrae during the process of their excavation with Prof. Roberto Abel of the Carlos Ameghino Provincial Museum of Cipolletti, Rio Negro Province, Argentina.

b. A closer view of the same part of the vertebral column.

In both views, the vertebrae are oriented with the centrum towards the top and the neural arches to the bottom.

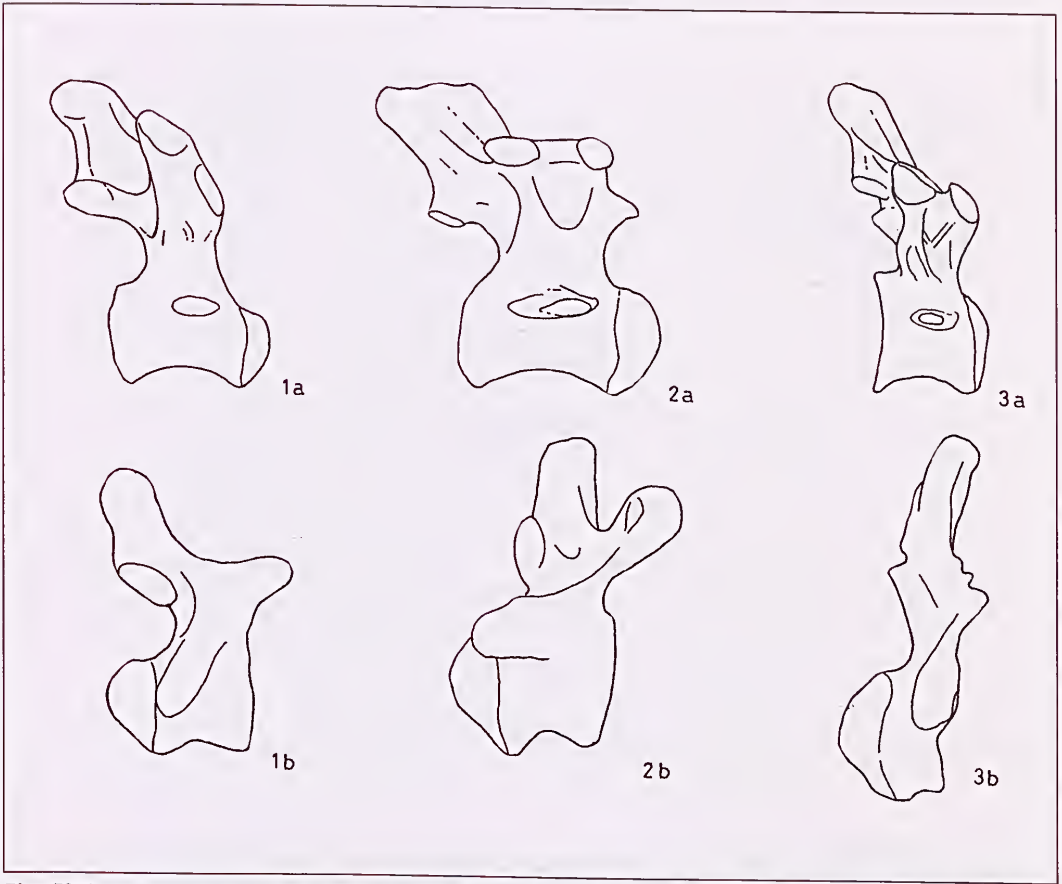


Plate 73. Comparative diagram of the vertebrae of (1) *Saltasaurus loricatus*, Saltasaurinae, (2) Titanosaurinae indet. from Brazil, Titanosauridae, and (3) *Argryosaurus superbus?*, Argryosaurinae all drawn to the same size.
a. Medial dorsal vertebrae.
b. Anterior caudal vertebrae.

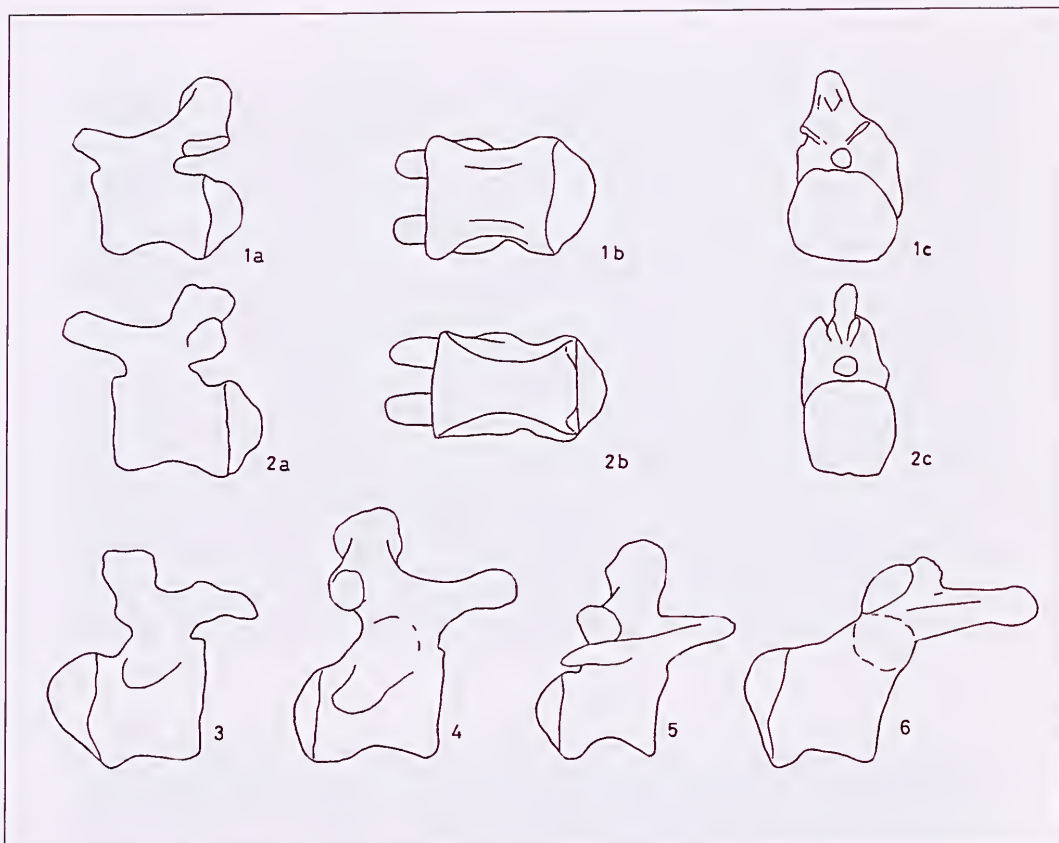


Plate 74. Comparative diagram of the medial caudal vertebrae all drawn to the same size.

1. *Neuquensaurus australis* n. gen. n. comb. (Saltasaurinae) in (a) lateral, (b) ventral and (c) posterior views.
2. Cf. *Titanosaurus* (Titanosaurinae) in (a) lateral, (b) ventral, and (c) posterior views.
3. *Alamosaurus sanjuanensis* Gilmore 1922 in lateral view.
4. Cf. *Titanosaurus* sp. (Titanosaurinae) in lateral view.
5. Titanosaurinae indet. in lateral view.
6. *Aeolosaurus rionegrinus* (Titanosaurinae) in lateral view.

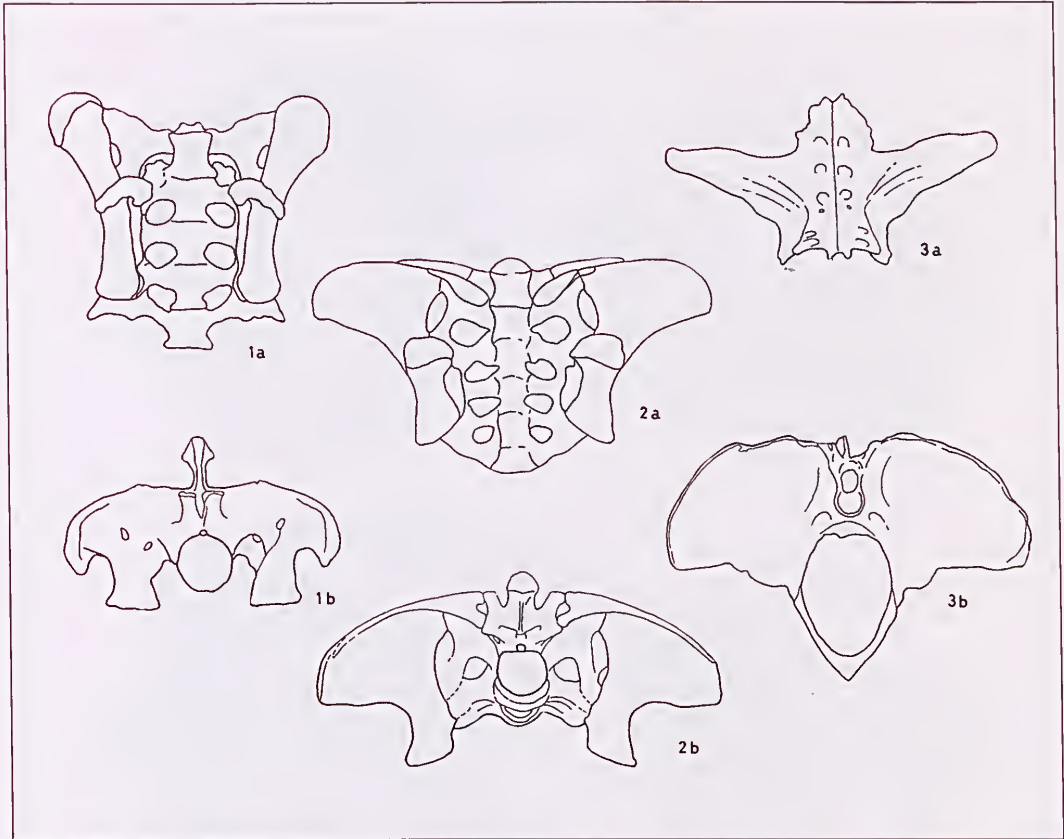


Plate 75. Comparative diagram of the morphology of the pelvic girdle of *Haplocanthosaurus* in (1a) lateral and (1b) anterior views; Titanosauridae indet. from Peirópolis, Brazil in (2a) ventral and (2b) anterior views; *Paramylodon* in (3a) dorsal and (3b) anterior views.

Figures 1a and 1b after Hatcher (1903). Figures 3a and 3b after Stock (1925).

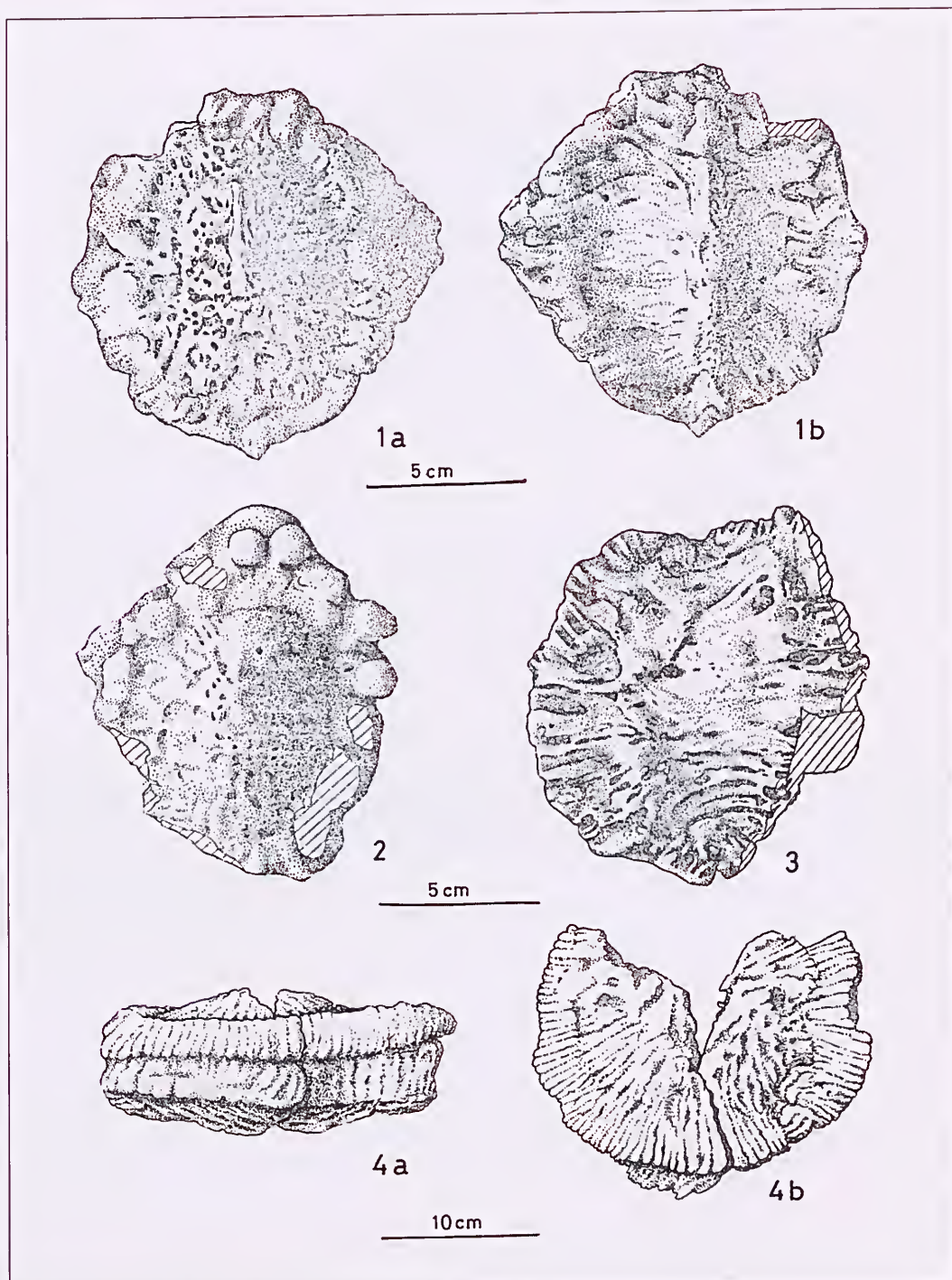


Plate 76. *Saltasaurus loricatus* Bonaparte and Powell 1980.

1. Dermal plate, PVL 4017-112, in (a) external and (b) internal views.

2. Dermal plate, PVL 4017-115, in external view which shows a subcircular area of bony cells related to fusion along the margins.

3. Dermal plate, PVL 4017-134, in internal view

Titanosaurus madagascariensis Depéret 1896

4. Dermal plate in (a) marginal and (b) external views. After Depéret (1896)

Drawn by E Guanuco.

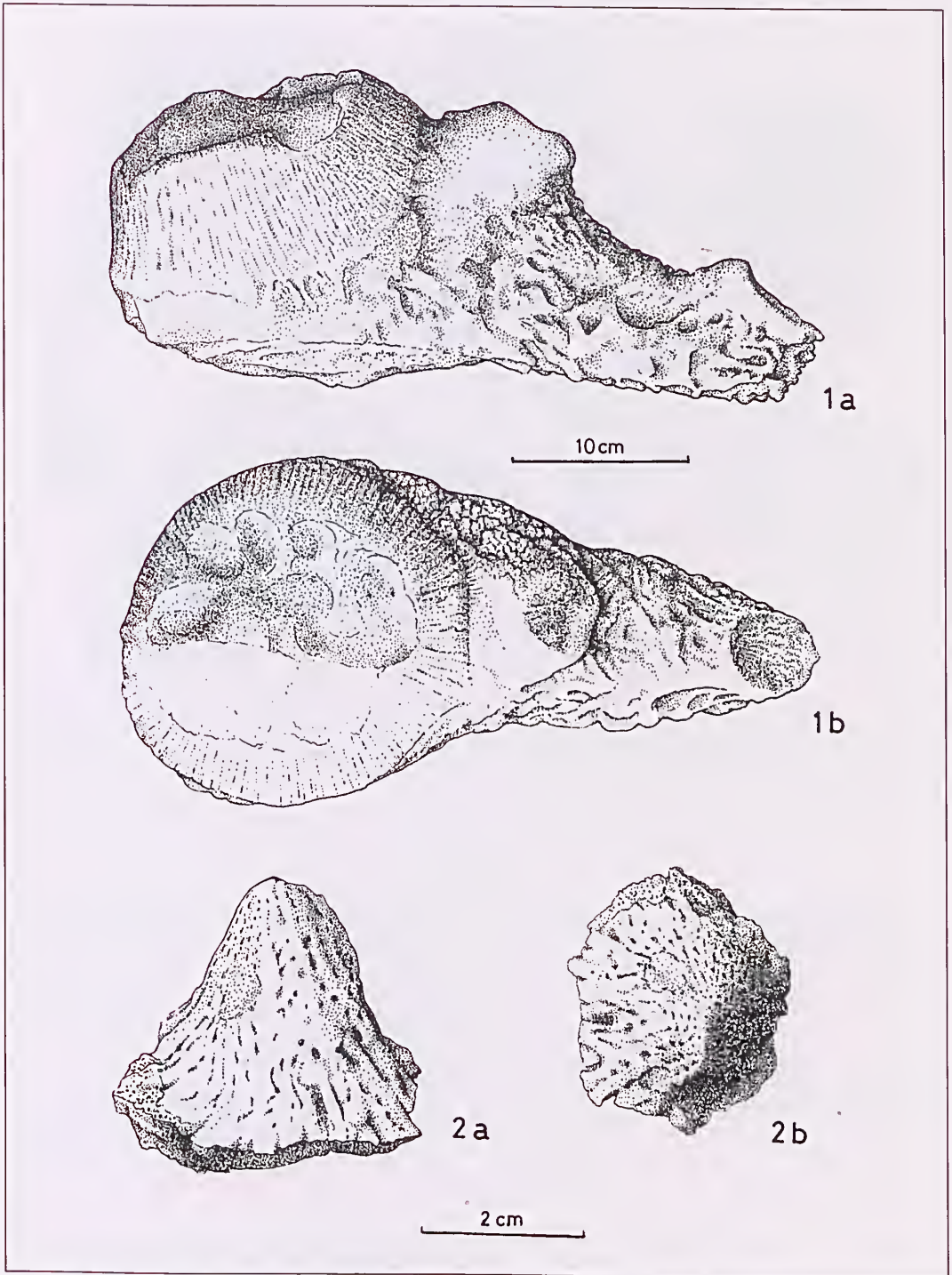


Plate 77. Titanosauridae indet.

1. Large dermal plate provisionally attributed to the Titanosauridae from the Salitral Moreno locality, Río Negro Province, Argentina, in (a) lateral and (b) external view.

2. Highly vascularised dermal plate attributed to the Titanosauridae in (a) lateral and (b) external views.

Drawn by E Guanuco.

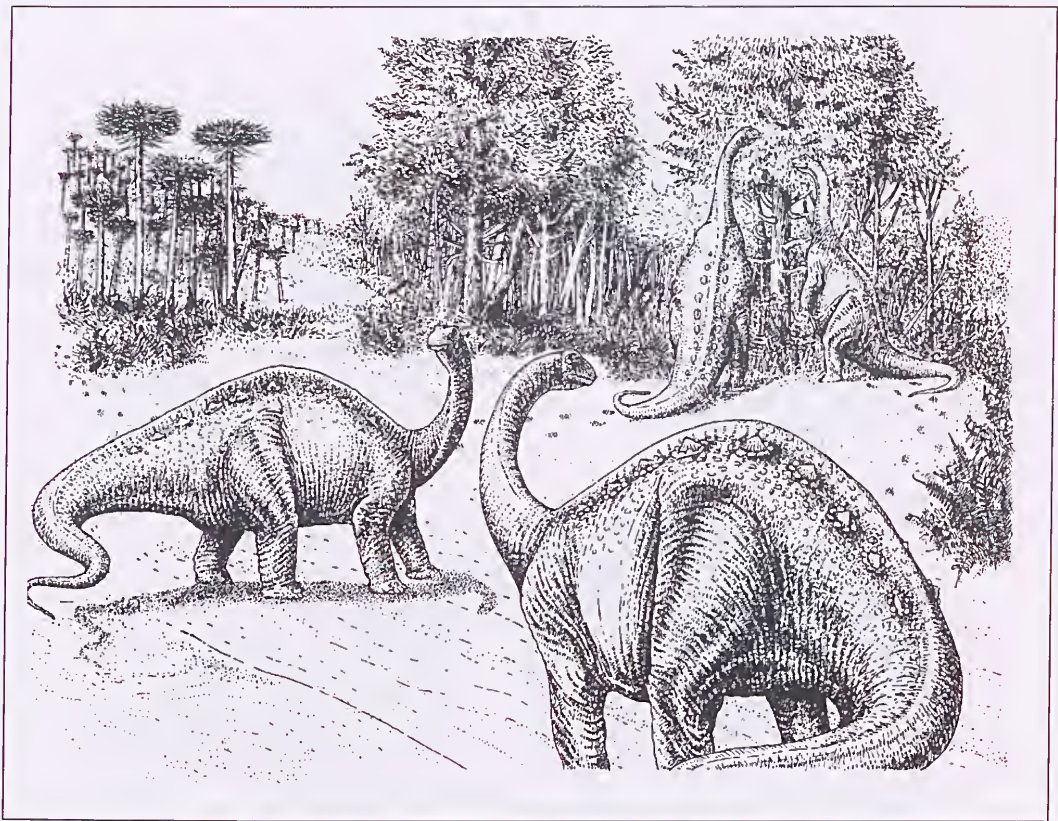


Plate 78. *Saltasaurus loricatus*. Reconstruction of a group of these titanosaurid dinosaurs in a Late Cretaceous environment. Drawn by E Guanuco.

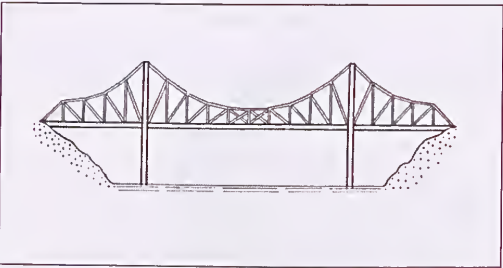


Plate 79. Cantilevered bridge (after Hildebrand 1974). Reprinted by permission of John Wiley & Sons, Inc.

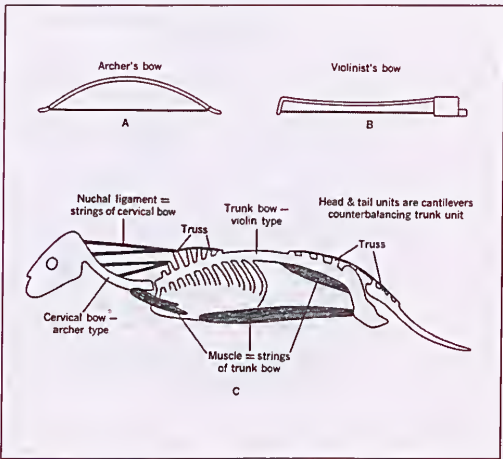


Plate 80. Model of the system of arches and cables that support the body (after Hildebrand 1974). Reprinted by permission of John Wiley & Sons, Inc.

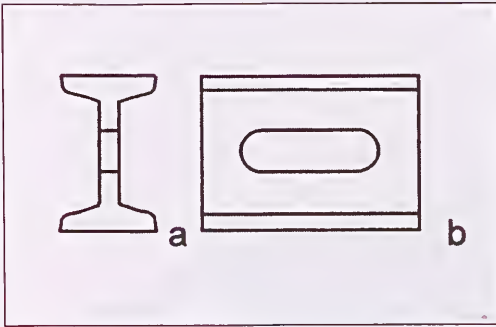


Plate 81. I-beam in (a) cross-section showing (b) an opening in vertical plate that does not compromise the strength of the structure.

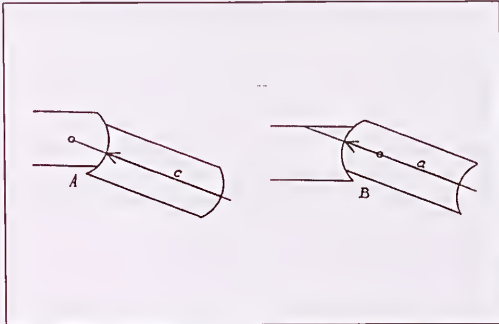


Plate 82. Diagram illustrating the biomechanical differences between (a) prococelous and (b) ophisthocelous caudal vertebrae when forces are applied in the cranial direction and the tail is flexed (after Troxell 1925).

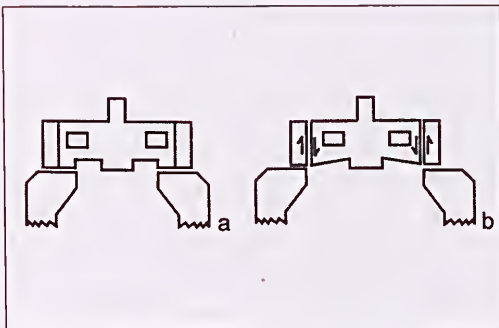


Plate 83. Diagram illustrating the iliofemoral articular relationships in (a) titanosaurs and other sauropods in contrast to (b) a model of a common reptile.

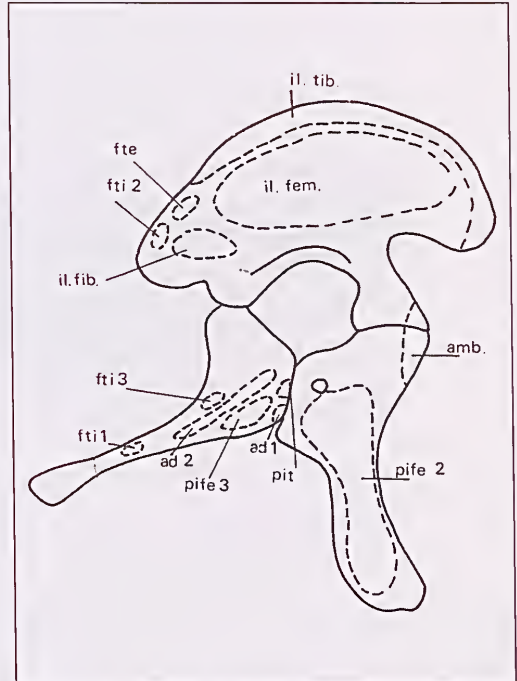


Plate 84. Main muscles of the pelvis of the sauropod *Camarasaurus*, according to the interpretation of Romer (1923).

Abbreviations; ad.: adductor; amb.: ambiens; fte.: external tibial flexor; fti.: internal tibial flexor; il. fem.: iliofemoral; il. fib.: iliofibular; il. tib.: iliotibial; pife: external puboischiofemoral; pit.: pubo tibialis.

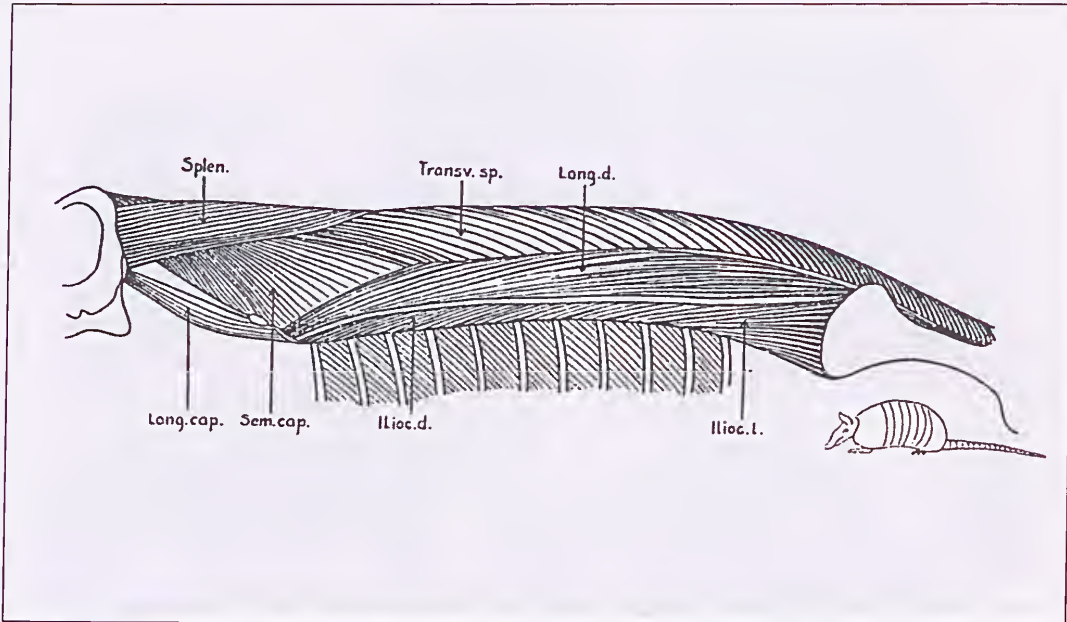


Plate 85. Epaxial musculature of *Dasypus novemcinctus*, showing the relation of the *m. iliocostalis lumborum* and *m. longissimus dorsi*. After Slijper (1946).
Abbreviations: Ilioc. d.: *m. iliocostalis dorsi*; Ilioc. l.: *m. iliocostalis lumborum*; Long. cap.: *m. longissimus capitis*; Sem. cap.: *m. semispinalis capitis*; Splen.: *m. splenius*; Trans. sp.: *m. spinalis transversus*.

Patagosaur	00000	00000	0000	00000	00000	000??	00000	00000	000
Haplocanth	?0121	01111	1011	00000	00000	10000	0011?	?0000	000
Ophisthoco	?0?20	?2010	1?1?	?0010	00011	10?00	??111	10101	0?0
Andesaurus	??120	01110	1002	100?0	0???0	100??	?????	?????	?0?
Saltasauru	11011	12110	1011	21110	00001	11001	10111	10121	111
Argyrosaur	??01?	11010	1?0?	1?11?	?00??	?????	00??1	1???1	1??
Epachtosau	??021	02111	1112	10100	21011	100?1	????1	10121	000
Lirainasau	10121	12010	1111	10101	11110	10111	11121	11???1	101
Peiropolis	?0021	12010	1111	1010?	?0010	100??	?????	?01??	???
Titano_col	?0???	1?110	1000	?0100	00010	10???	00111	?012?	???
Alamosauru	1????	?????	????	?0101	0?010	100??	??11?	1????	???
Ampelosaur	0????	?20?1	??01	1010?	?0011	10???	??111	1?0?1	111
Aeolosauru	??0??	?????	????	?011?	?00?1	10???	10???	1????	?1?
;									
ccode -2 20 23 38;									

Plate 86. Data matrix for titanosaurs (see text for explanation).

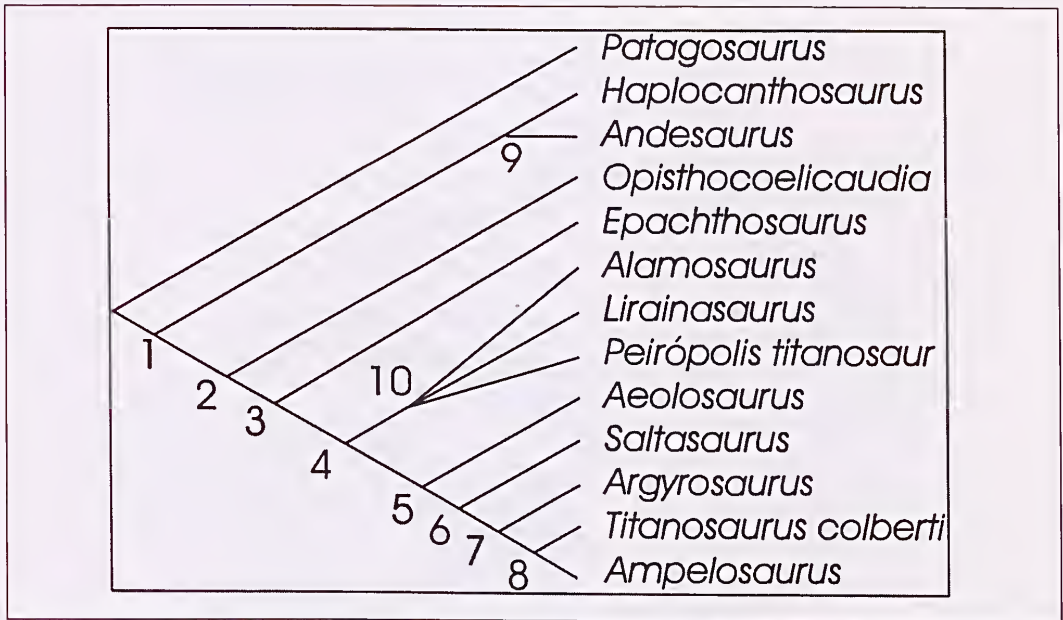
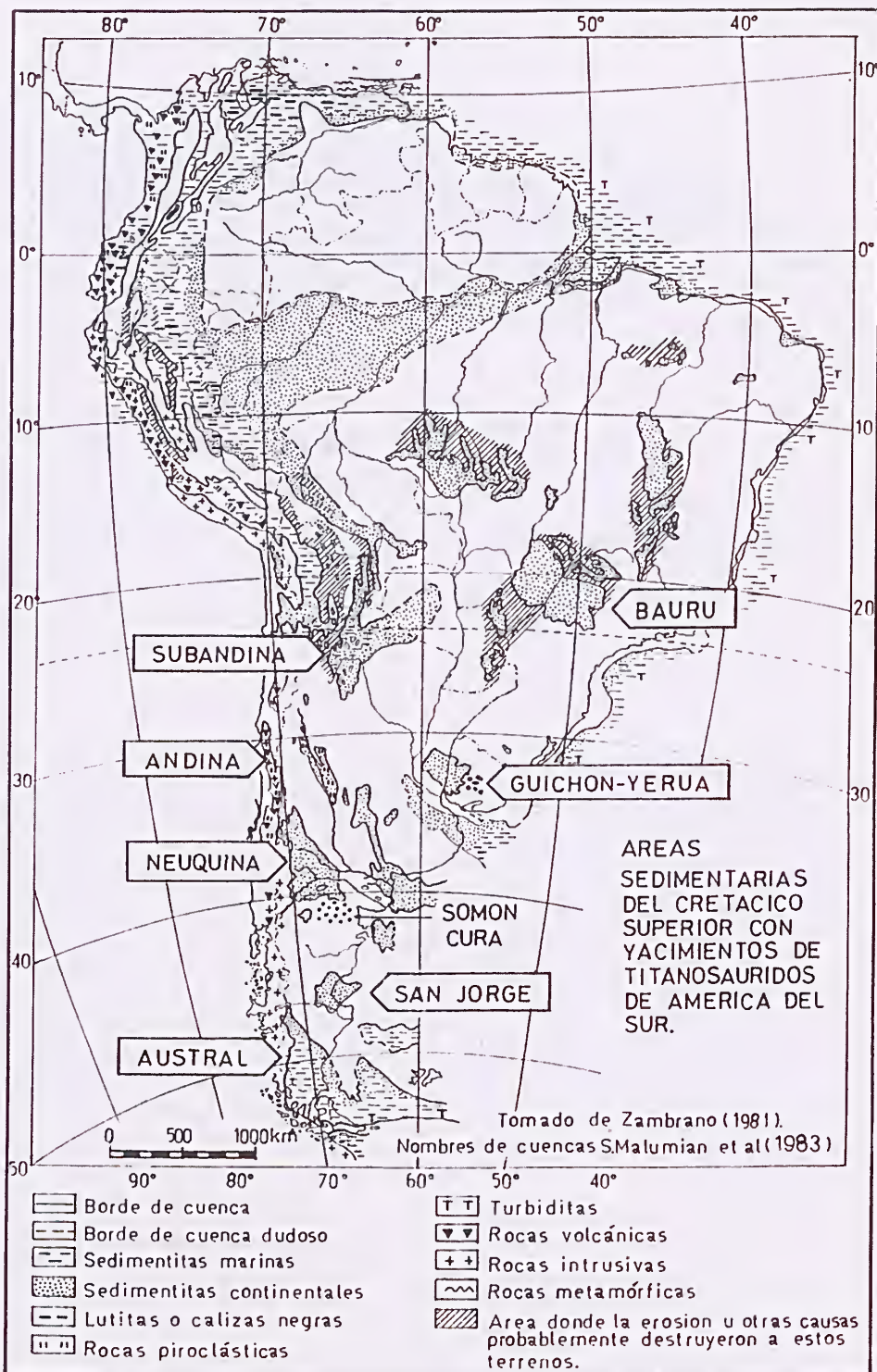
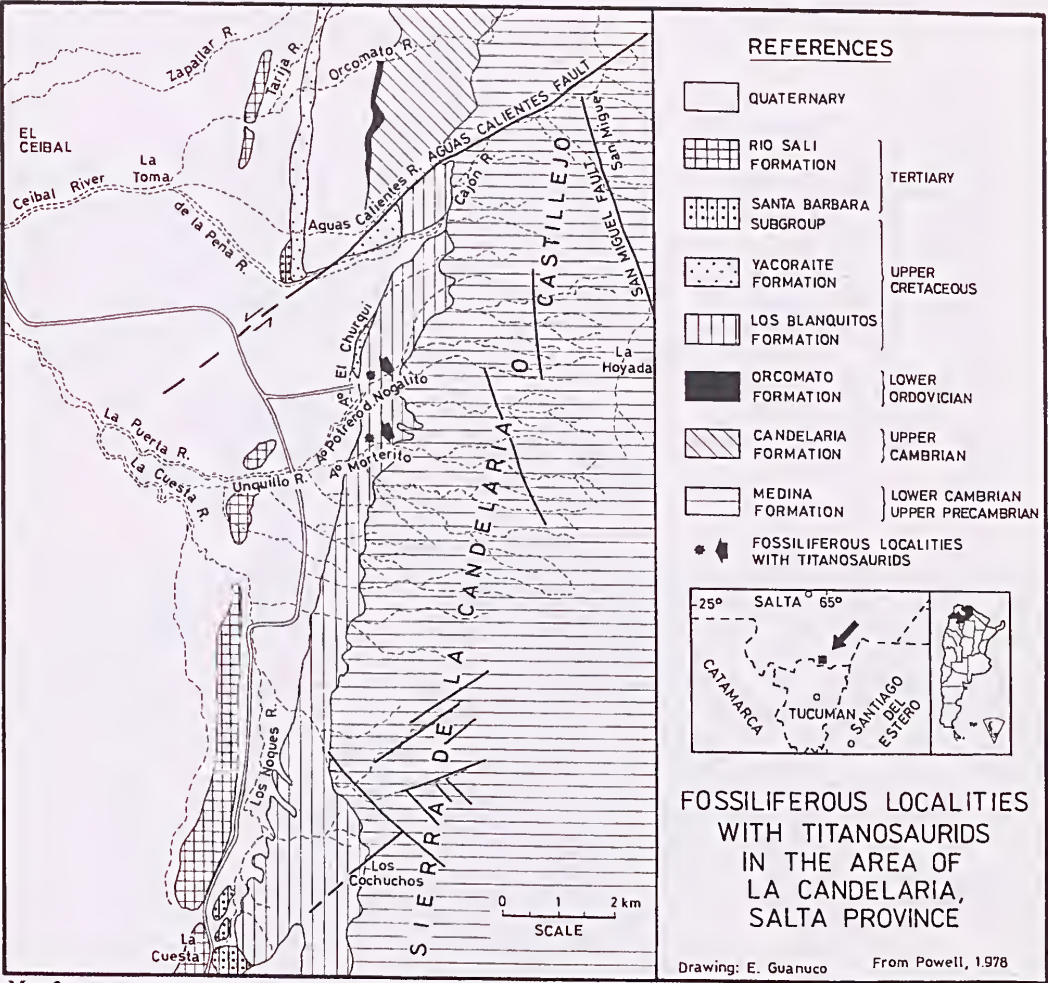
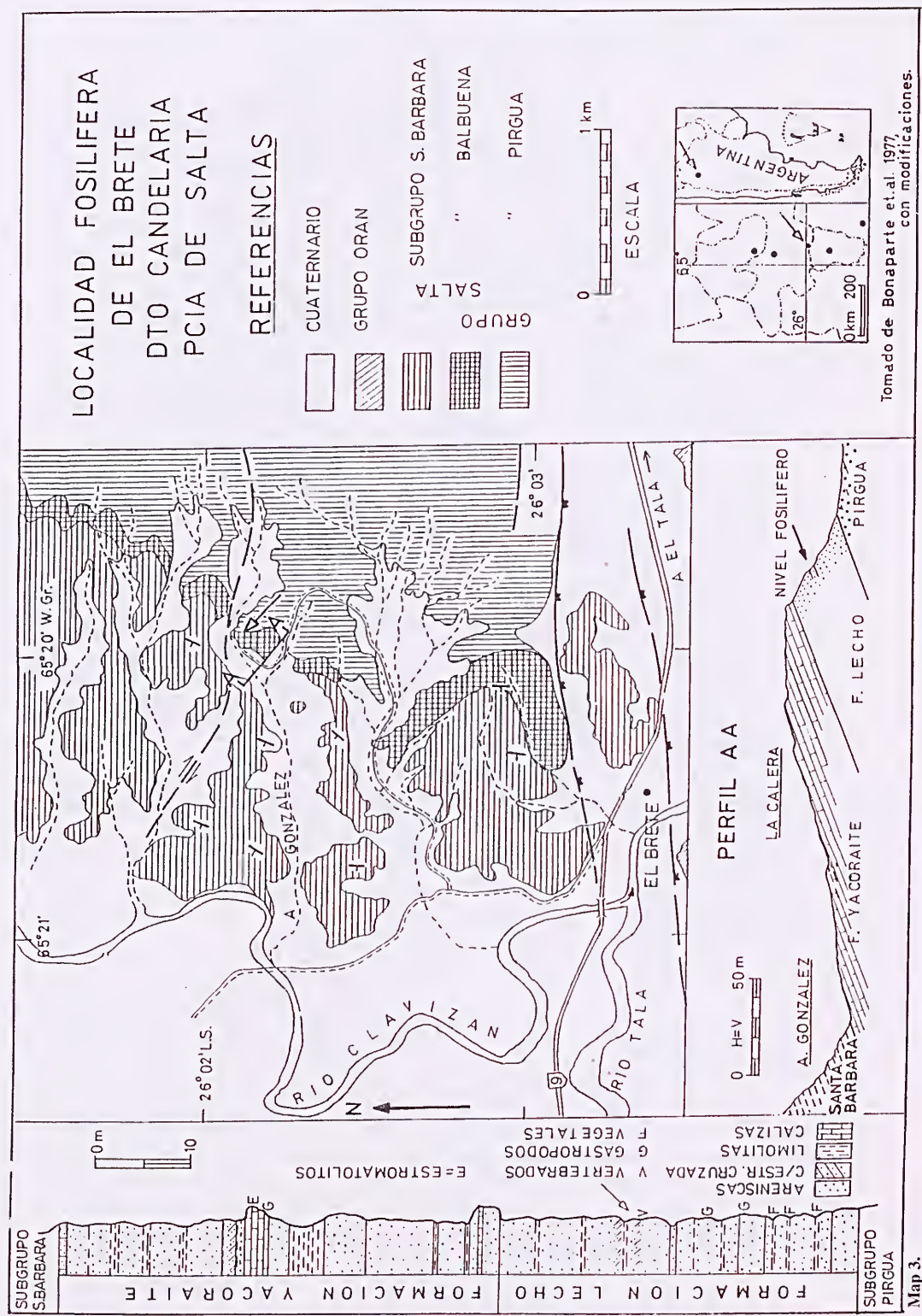


Plate 87. Cladogram of titanosaur relationships based on analysis of data presented in Pl. 86.

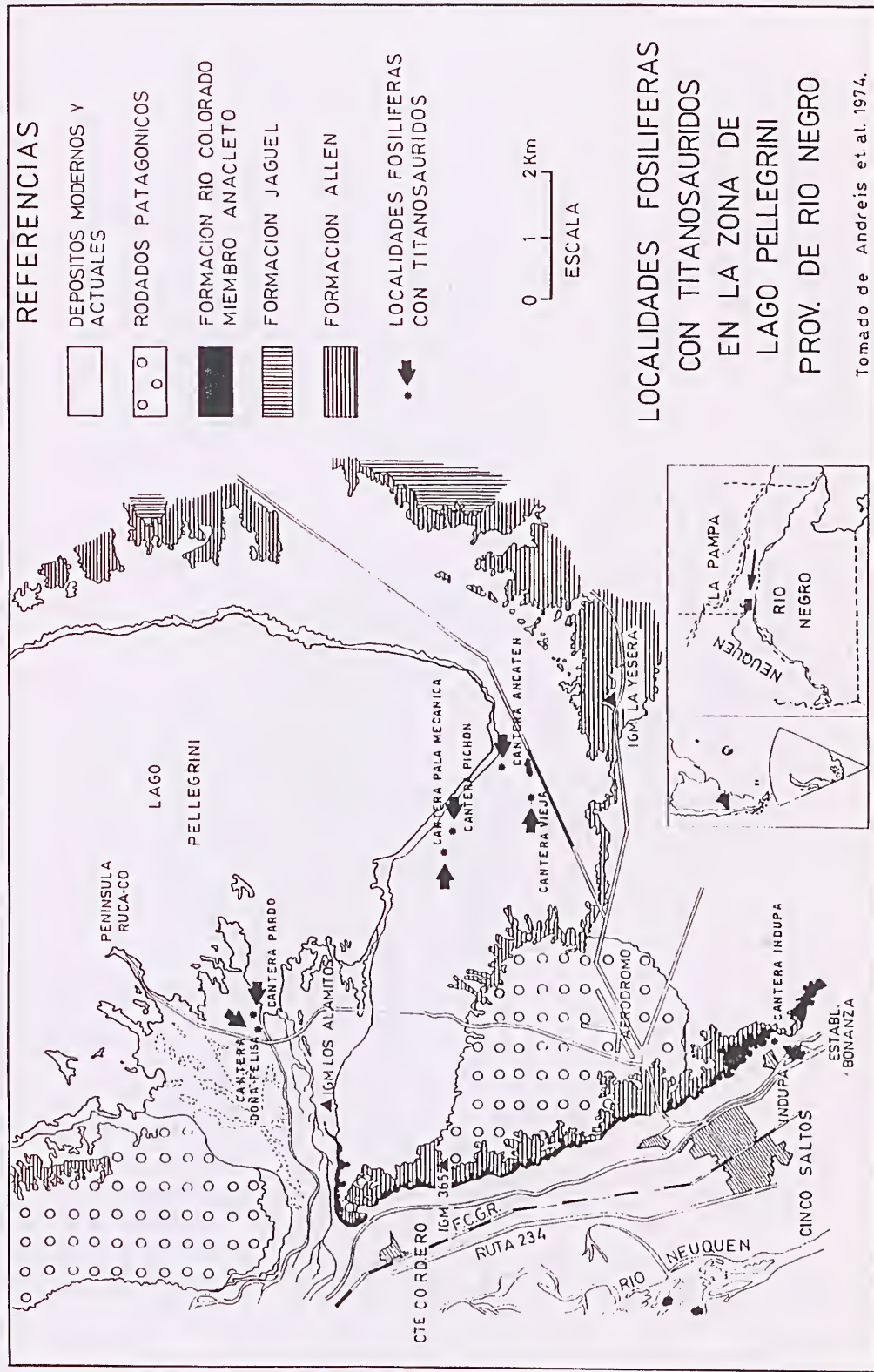


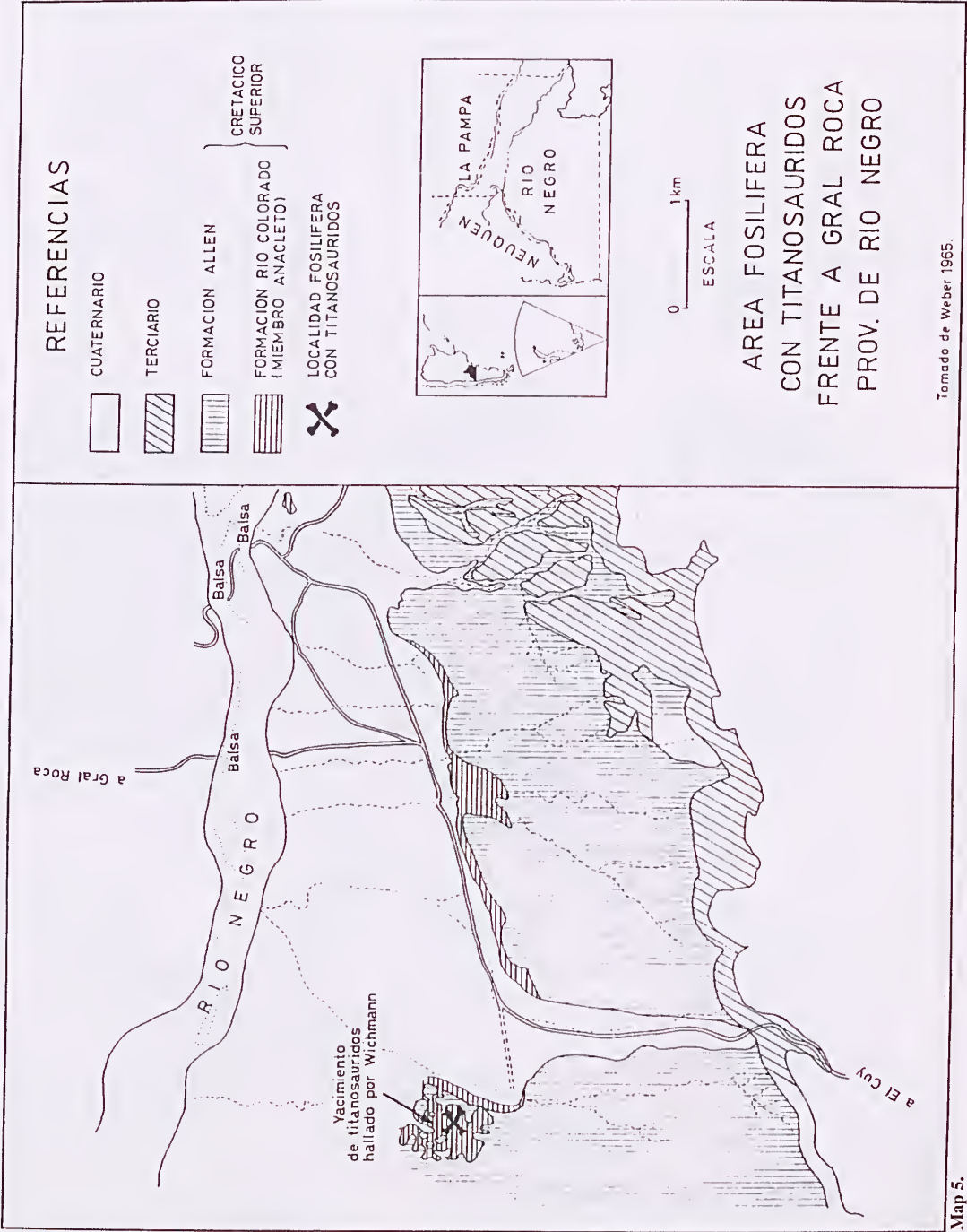
Map 1.





Tomado de Bonaparte et al. 1977, con modificaciones.

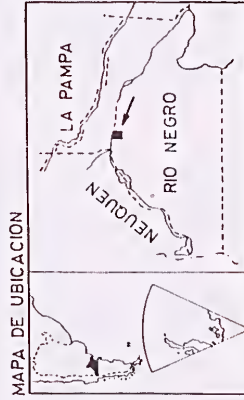




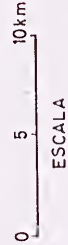
Tomado de Weber 1965.

Map 5.

LOCALIDADES FOSILIFERAS CON TITANOSAURIDOS EN LAS ZONAS DE SALITRAL MORENO Y SALITRAL OJO DE AGUA, PROV. DE RIO NEGRO

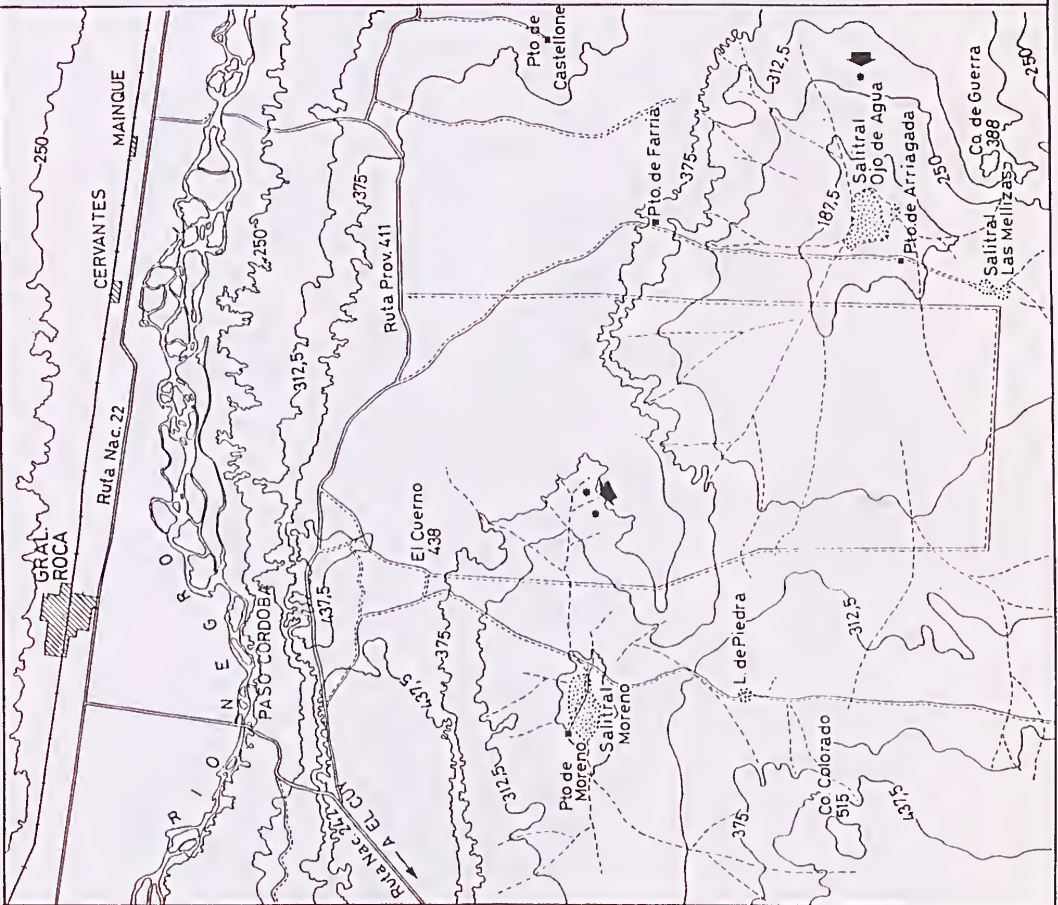


CURVAS DE NIVEL: EQUIDISTANCIA 62,5 mts

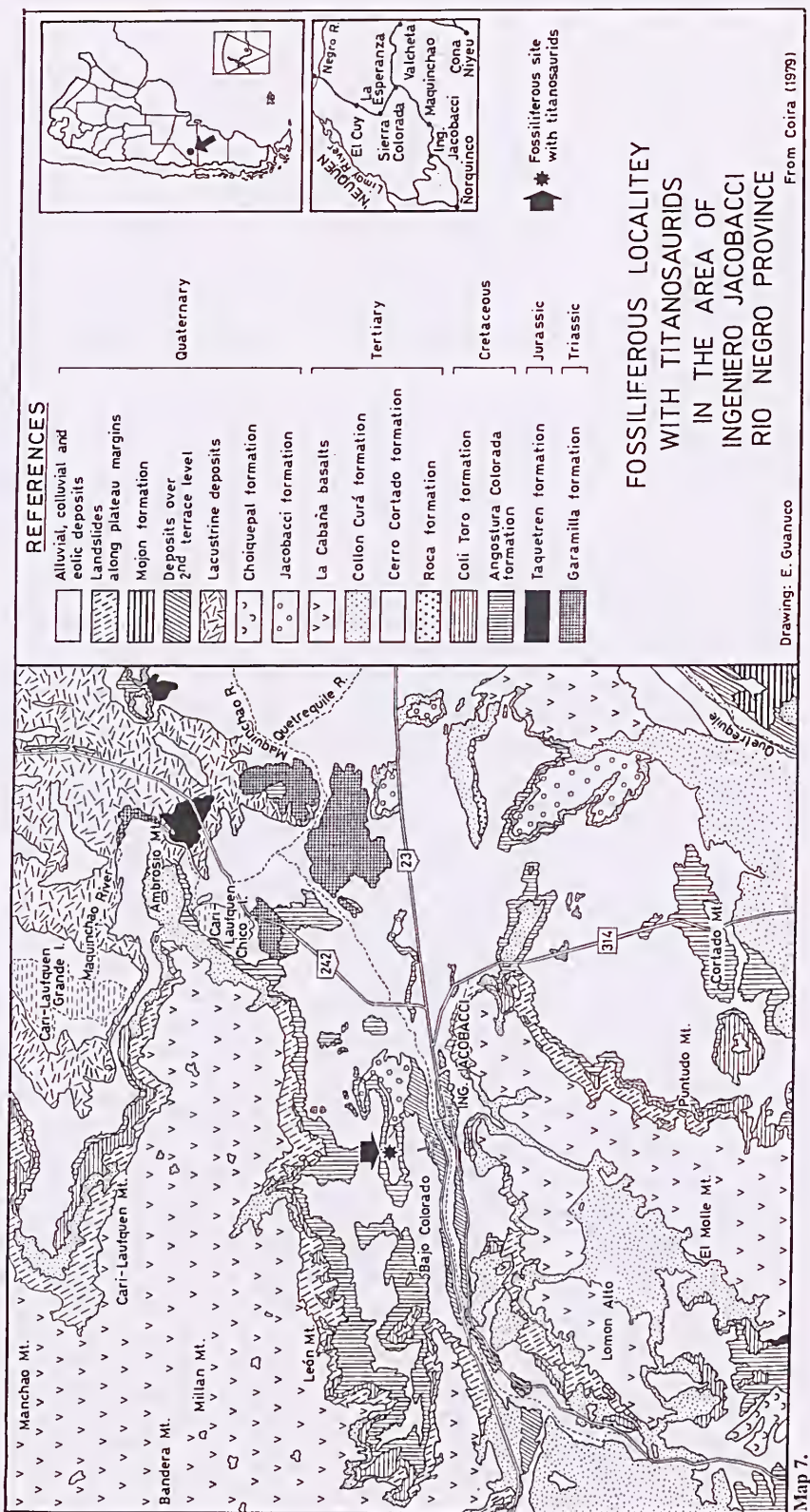


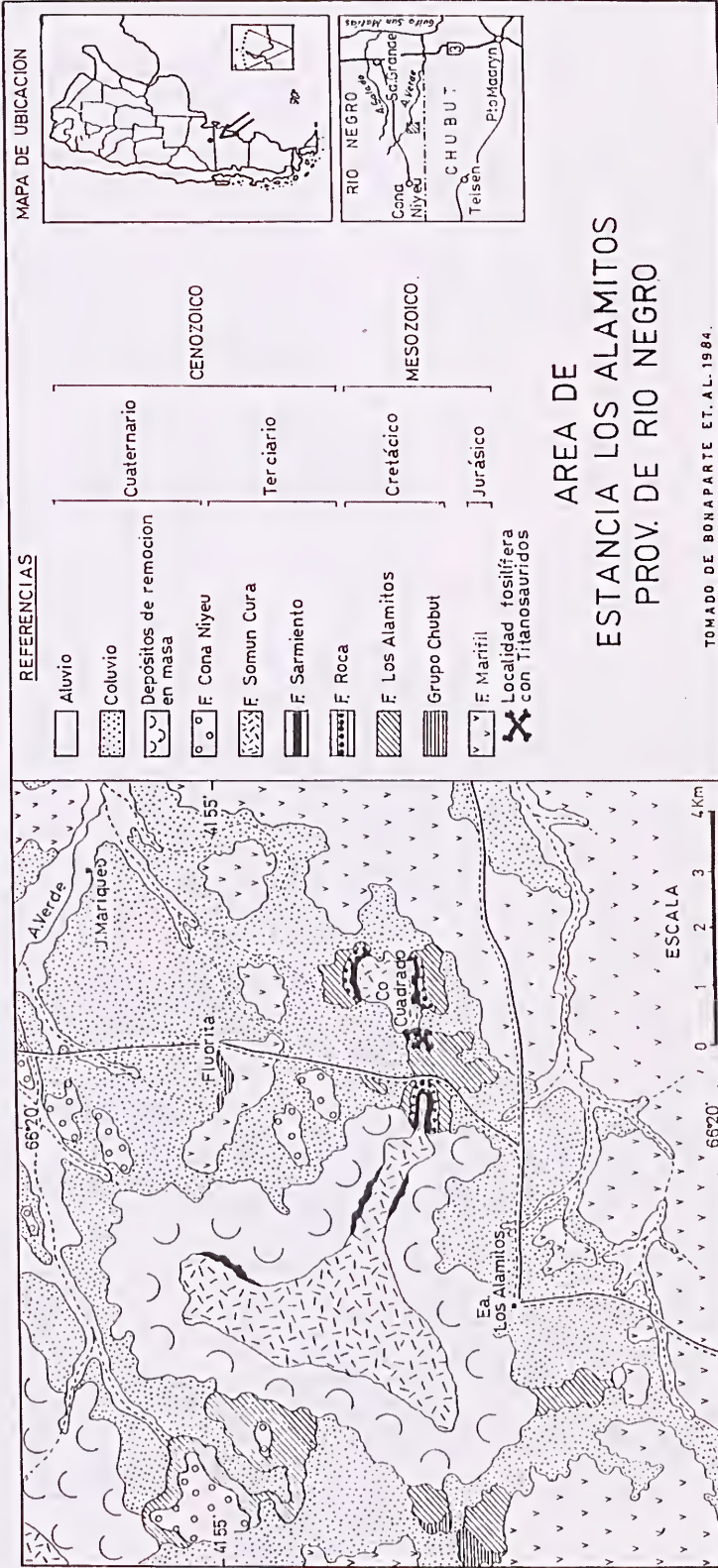
● LOCALIDADES FOSILIFERAS
CON TITANOSAURIDOS

Tomado de Hoja 36f Gral. Roca-Direc. Nac. de
Geol. y Min. Dto de Geografía, Río Negro.

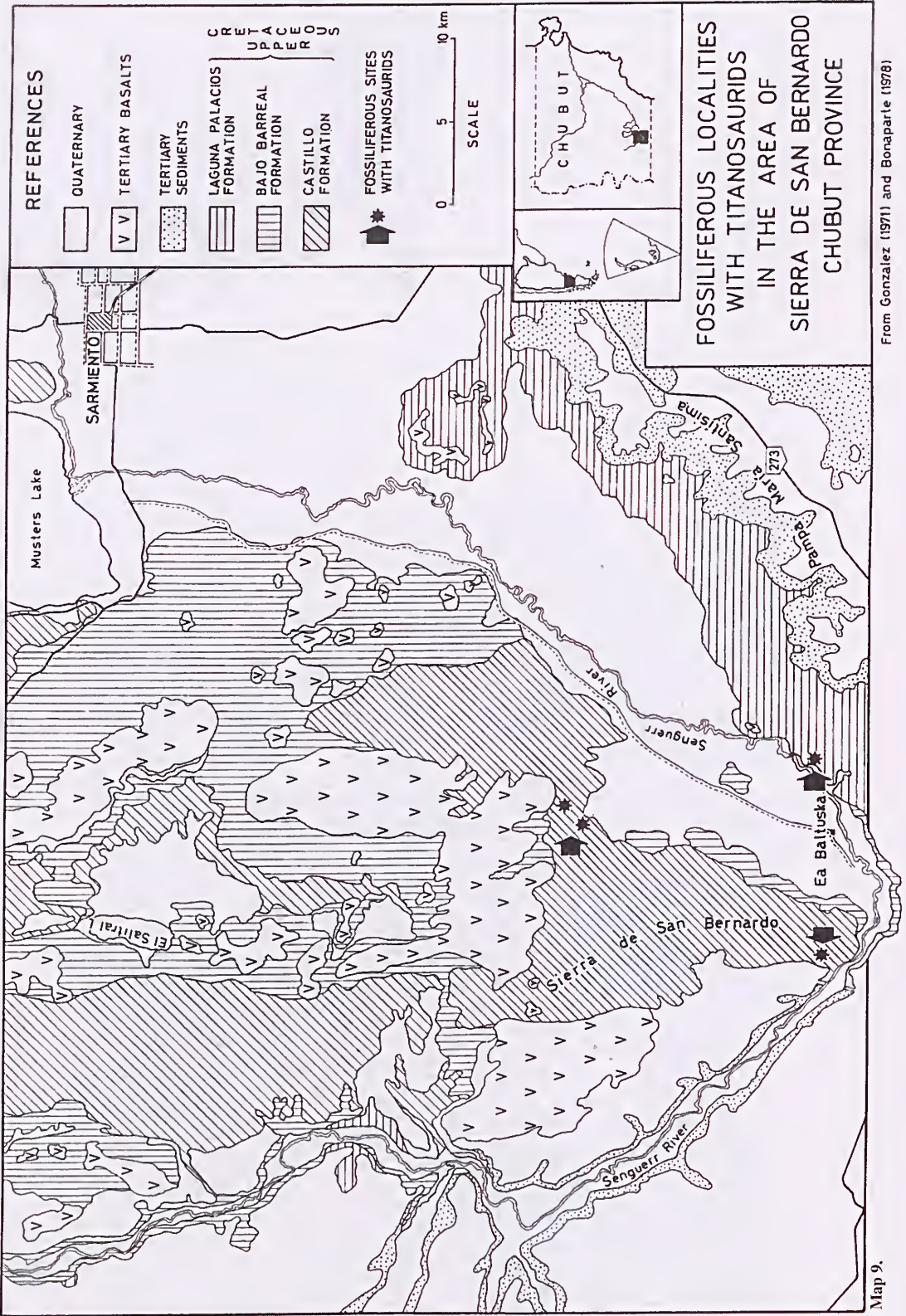


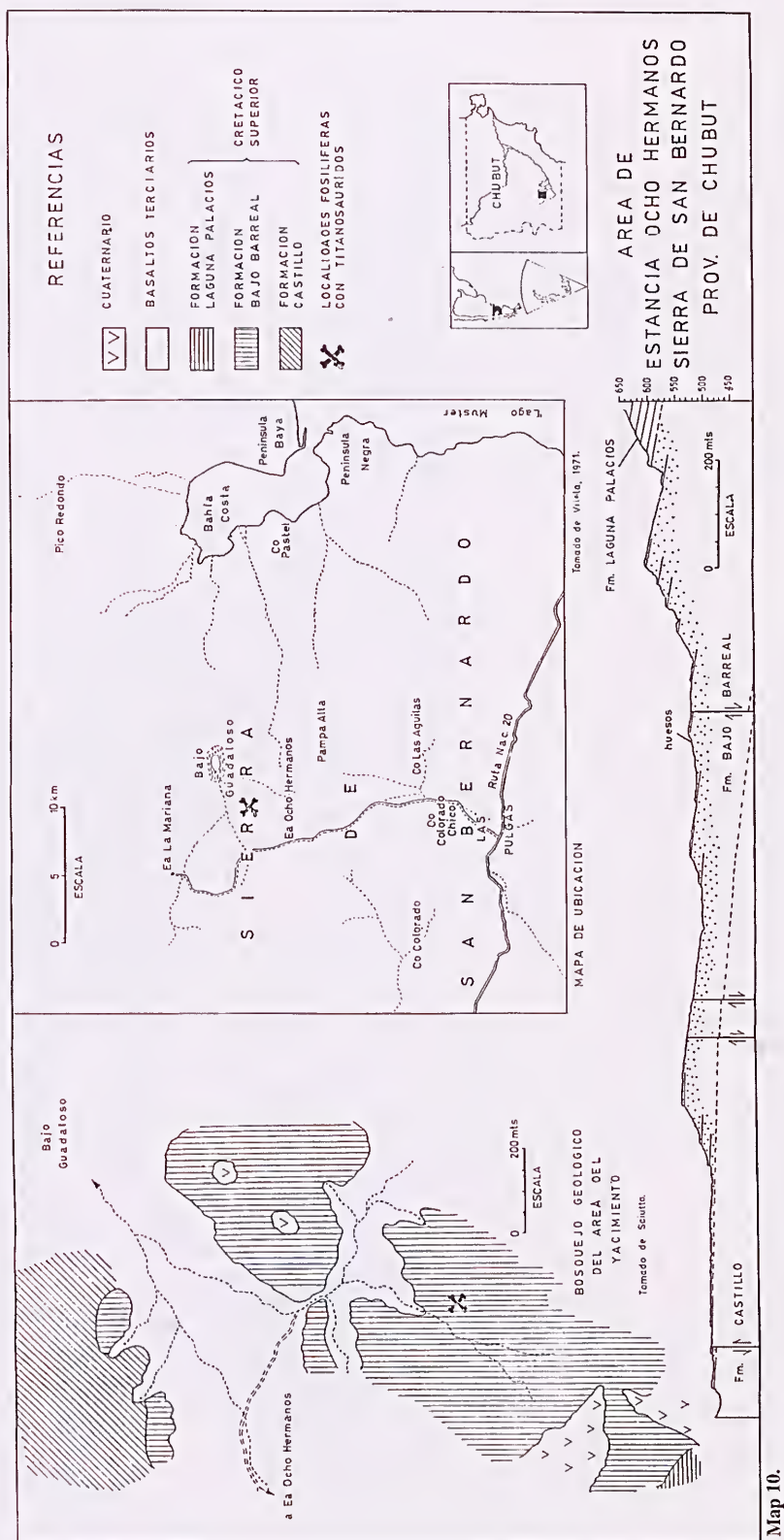
Map 6.

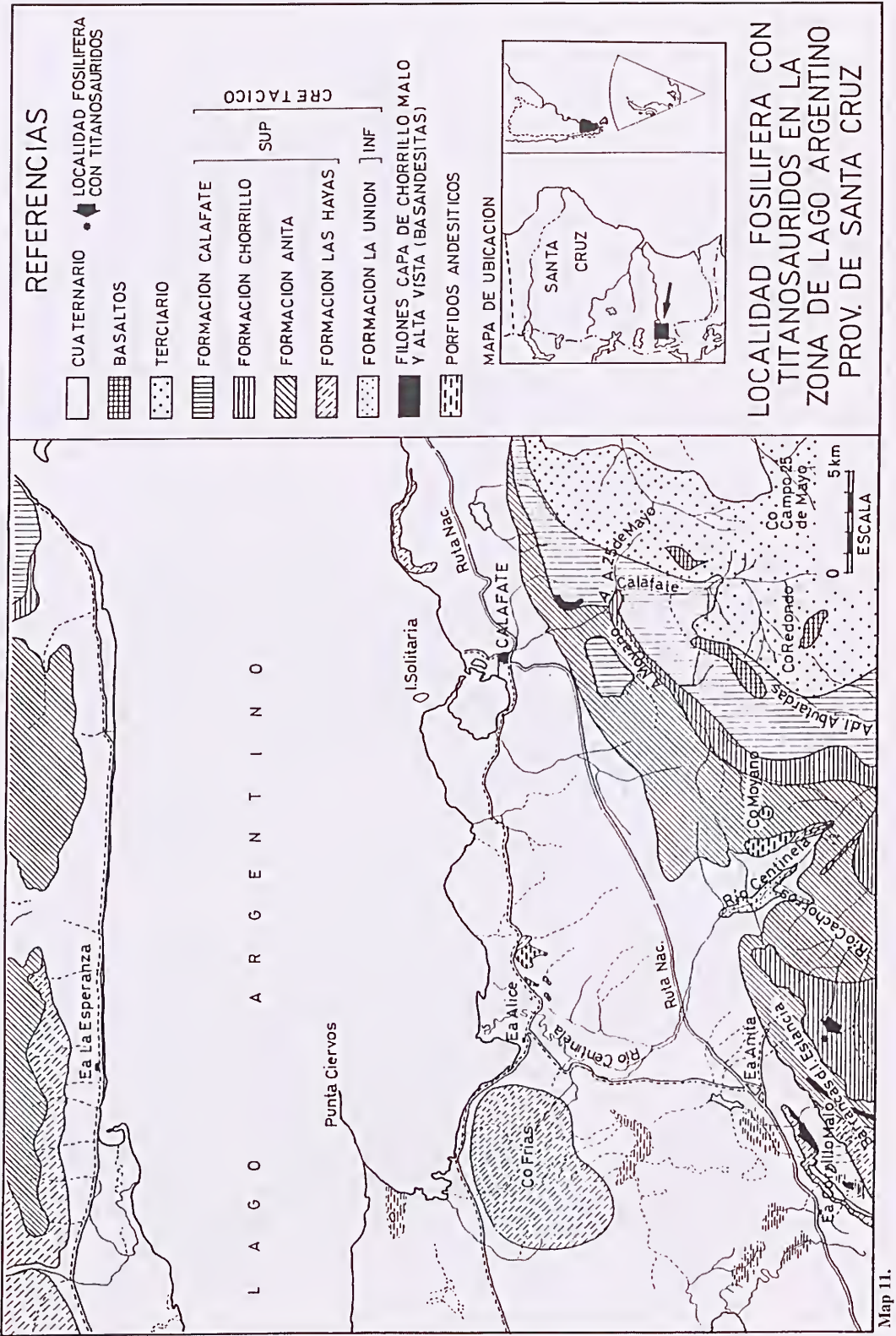


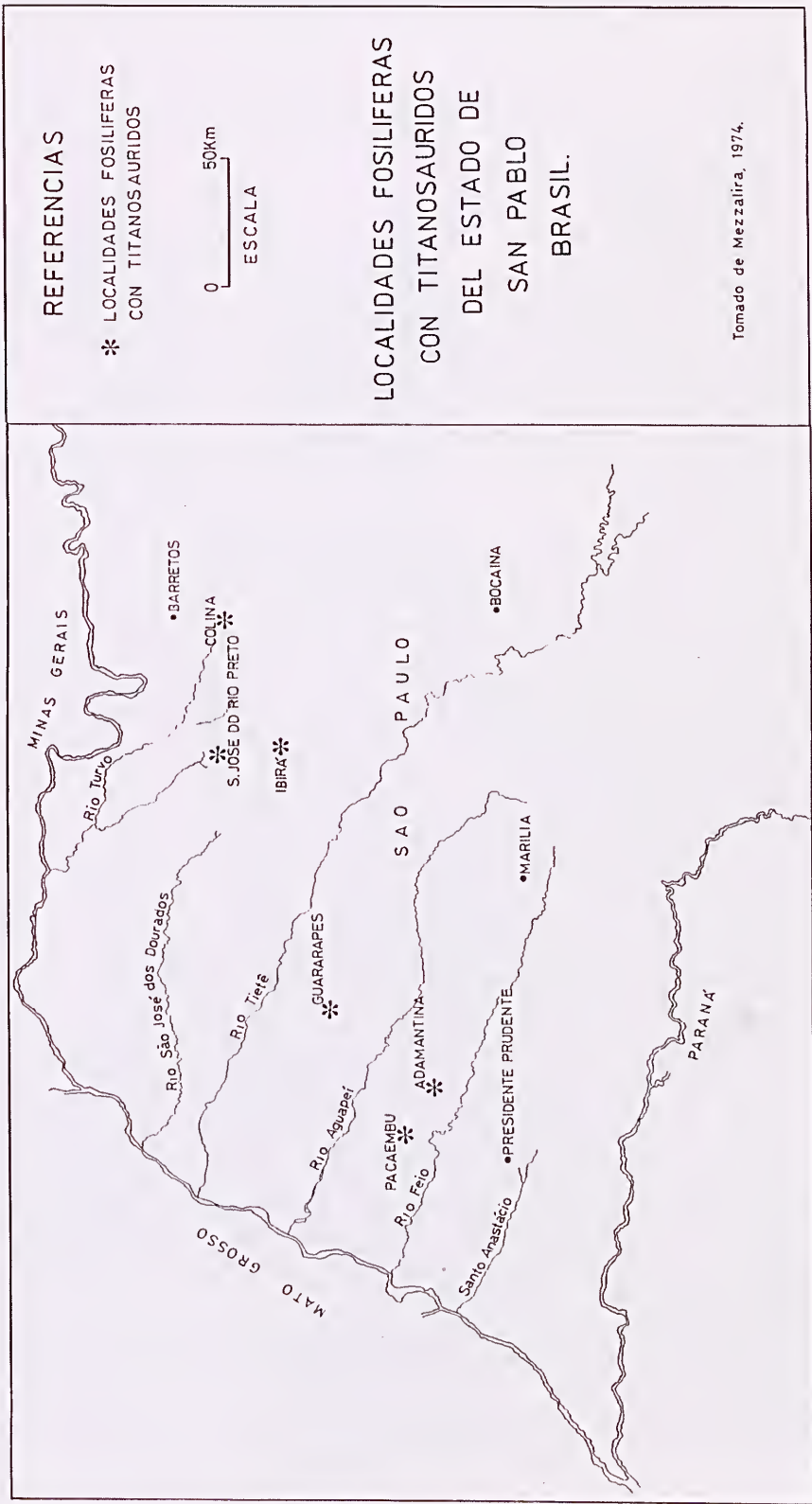


Map 8.

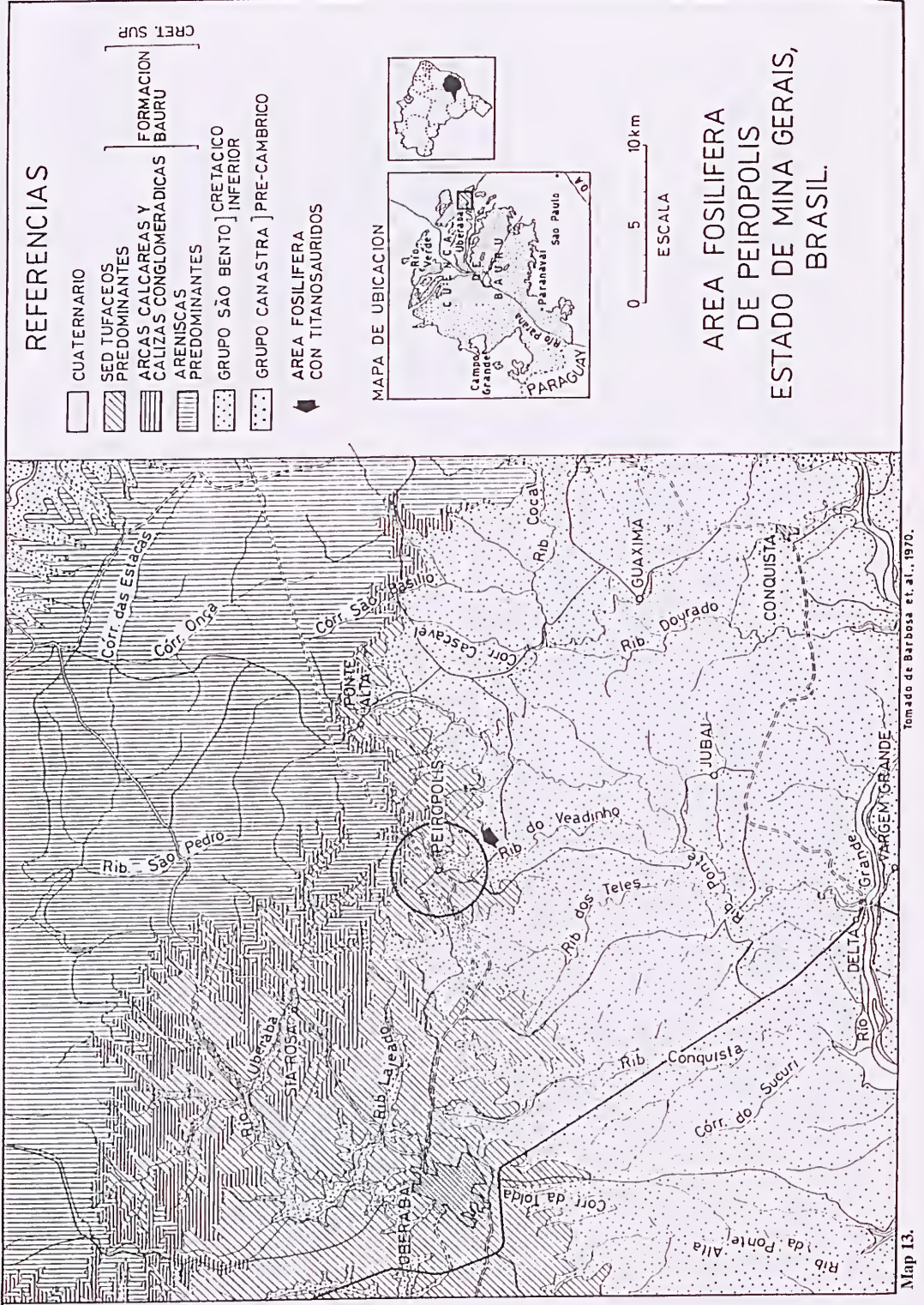


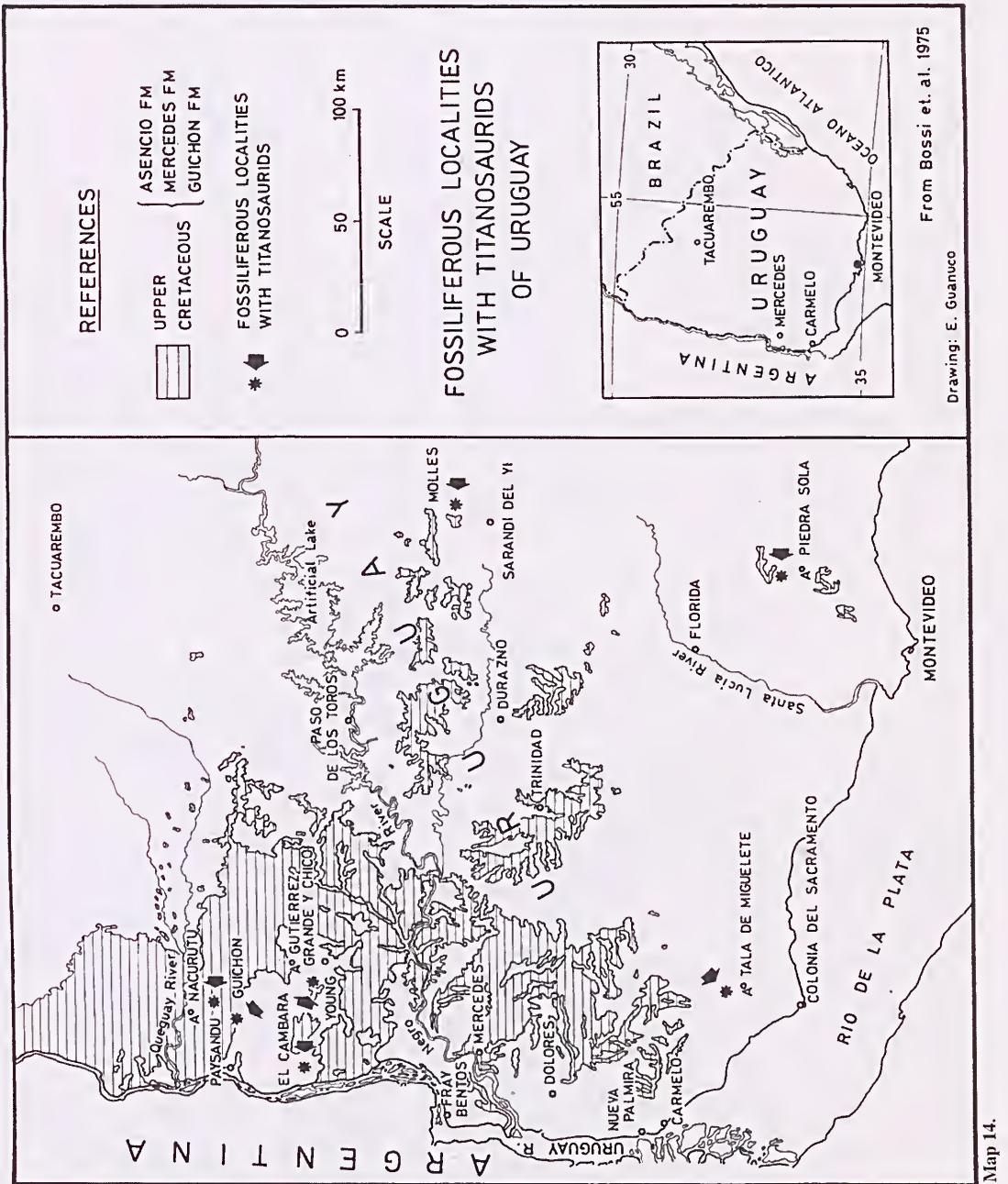




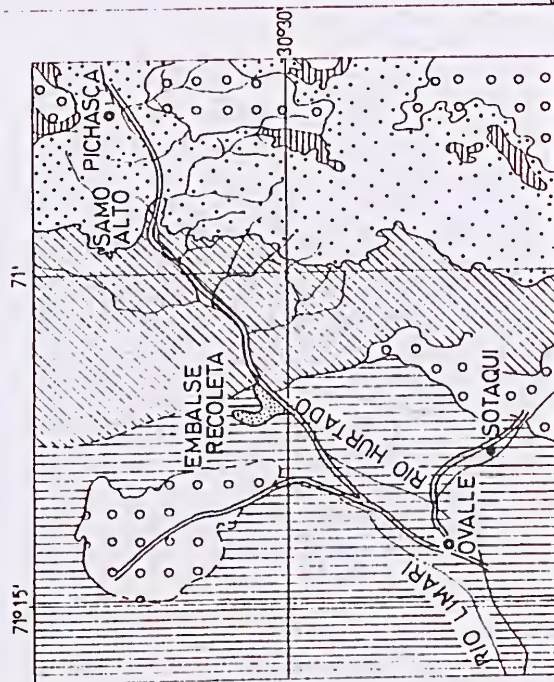


Map 12.





LOCALIDAD FOSILIFERA DE PICHASCA PROV. DE COQUIMBO, CHILE

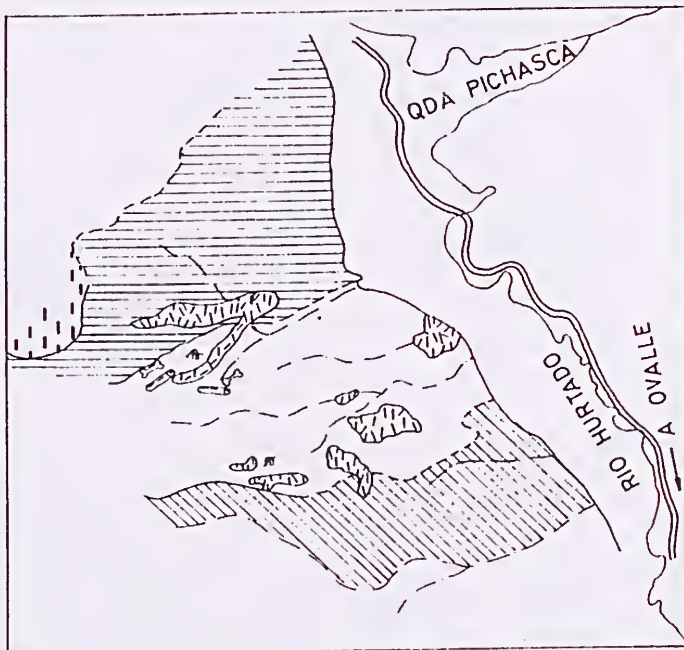


ESCALA 1:250,000

- Formación Los Elquiños
- Formación Vinita
- Formación Quebrada Marquesa
- Formación Arqueros
- Rocas Intrusivas
- Cretácico Sup.
- Terciario Inf.
- Cretácico Inf.

Tomado de Casamiquela et al., (1969).

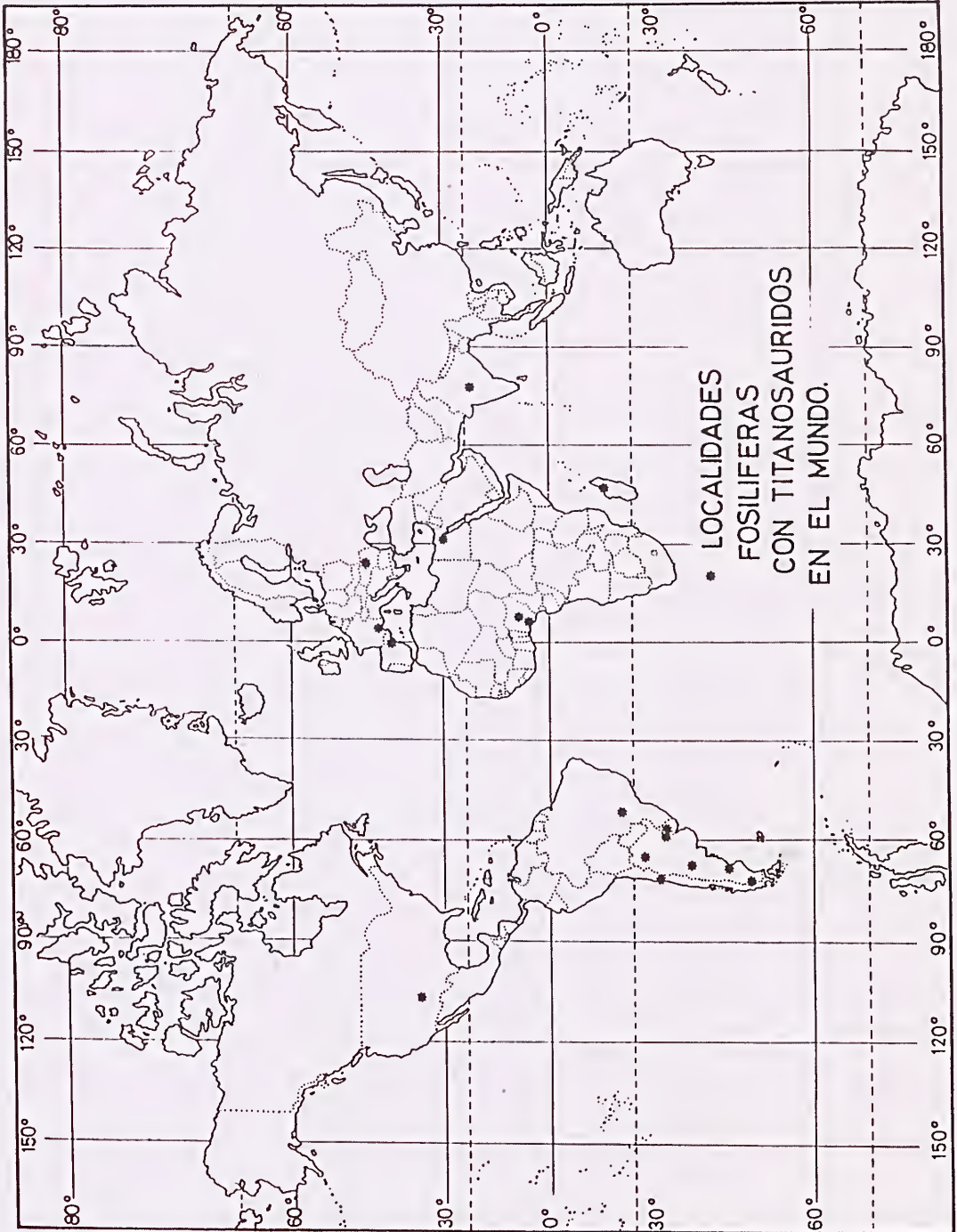
CROQUIS GEOLOGICO DEL AREA DE PICHASCA



ESCALA 1:250,000

- Porfidos intrusivos
- Ignimbrita
- Areniscas y conglomerados de colores claros.
- Conglomerados grises
- Areniscas conglomerados y lutitas de color rojo con huesos troncos hojas y tallos fósiles.
- Huesos
- Restos de troncos
- Tallos y hojas

Map 15.



Map 16.